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AT HARVARD COLLEGE

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THE PALATINE PROCESS OF THE PREMAXILLA IN
THE PASSERES

A study of the variation, function, evolution and
taxonomic value of a single character
throughout an avian order

BY WALTER J. BOCK

Biological Laboratories, Harvard University

CAMBRIDGE, MASS., U.S.A.
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INTRODUCTION

Ever since the beginnings of avian taxonomy, ornithologists have concentrated on the species problem, with the study skin as the traditional object of study. This was in many ways a fortunate choice, and as a result, avian systematics on the species level is today the most advanced area in the field of taxonomy. But at the same time, interest in the higher categories of birds has lagged so far behind that we know virtually nothing about the affinities of most groups of birds. Even now, most systematic work on the supergeneric level represents scarcely more than guesswork, there is little agreement on the limits of the orders or on their relationships, and within the relatively sharply defined orders, the arrangements of the families are, at best, obscure. Most neglected of all the orders are the Passeres which, although they contain about half of the recent species of birds, have received less attention than any other group. The lack of interest in the anatomy as well as in the classification of the perching birds dates back to the beginnings of ornithology and is reflected in the attitude of the standard texts (Fürbringer, 1888; Gadow,

1891-93; and Beddard, 1898). These authors give detailed coverage of the families and even subfamilies of the non-passerine birds, yet they barely distinguish between the suborders of the perching birds, the tacit assumption being that their highly uniform morphology precludes the use of comparative anatomy as a basis for their classification. Unfortunately, this high degree of morphological similarity has usually been interpreted as uniformity, with the conclusion that comparative anatomical studies are of no use whatsoever in untangling the relationships within the Passeres.

Recently, there has been a revival of interest in the Passeres, as is indicated by the publication of a number of papers on their anatomy (Arvey, 1951; Ashley, 1941; Beecher, 1951a, 1951b, 1953; Berger, 1957; Engels, 1940; Fiedler, 1951; Hudson and Lanzillotti, 1955; Mayr, Andrew and Hinde, 1956; Moller, 1930, 1931; Nelson, 1954; Sims, 1955; Stalleup, 1954; Stonor, 1937, 1938, 1942; Sushkin, 1924, 1925, 1927, 1929; Swinebroad, 1954; and Tordoff, 1954a, 1954b). These papers have shown that the passerines are not absolutely uniform in their internal anatomy and that comparative anatomical studies may aid in the understanding of relationships on the familial level. With the removal of this psychological block and with increasing interest in the problems of passerine anatomy we may at last be on the way to understanding the evolution and classification of the perching birds.

This revival of interest in the Passeres is, however, not without its problems, of which the most important is the disagreement in interpretation of the morphological findings and their value in showing relationships. Stresemann (1959) has presented an excellent picture of the problems confronting avian systematics which should be read by every worker interested in this field. Mayr (1955, 1958) has discussed some of the perplexing evolutionary assumptions pertinent to passerine classification, and Starck (1959) has commented on some of the anatomical problems. These authors agree, more or less, that the major problems stem from the characters used as clues to relationships, and from uncritical use of the pertinent evolutionary and morphological principles. But something else is involved. Perhaps the difficulty arises from the relatively small degree of anatomical difference between passerine families; perhaps it stems from insufficient study of the characters or perhaps it is a result of the method by which the groups and their structures are compared. Undoubtedly, the answer is a combination of all three suggestions, but the

last one is probably the most important, and attention will therefore be focused on it.

The best approach in taxonomic studies is a comparison of as many characters as possible throughout the entire group. This ideal method is feasible only with comparatively small orders and families of birds. It is not practical when dealing with a large group such as the Passeres; alternate methods must be employed. These are of two types. The first is a comparison of as many characters as possible in two or more families. This is the method used in most of the works cited above. The second is an analysis of a single character or character-complex throughout the whole group under consideration. No proper study of this type has, to my knowledge, been made for the passerines. Therefore, this paper presents a sample study of a single character — the palatine process of the premaxilla — in the Passeres, as a basis on which some of the problems of passerine anatomy and classification may be explored.

The method of "single character study" is the analysis of all aspects of the character essential to understanding its evolution — this being the major goal of these studies. Although certain specialized aspects must be investigated in some cases, as for example, the embryology of the palatine process in this study, the following steps must be included in every "single character study."

a) A survey of the occurrence, structure and variation of the character must be undertaken. In general, the scope of the survey includes the next higher taxonomic category that contains the group under consideration. For instance, if the affinities of a passerine family are being studied, then the character must be surveyed throughout the Passeres. The degree of variation should be ascertained in each taxonomic group down to the species. All aspects of variation, e.g., sexual, age, geographical, must be separated and clearly distinguished from one another. Usually in studies of avian anatomy, it is not necessary to consider infrageneric variation, since most anatomical characters do not vary among congeneric species. This is especially true in the Passeres.

b) The functional significance of the character, including the meaning of its structural changes within the group, must be established. This is the most important part of the analysis of a taxonomic character and the one most often omitted or, if included, covered only in a superficial way. Because of limitations and technical difficulties, conclusions concerning the functions

are usually only deductions based on physical considerations of the morphology exhibited by the character. It is only rarely possible to observe the bird alive and to deduct the function from actual observations, or to conduct the necessary experiments to prove it conclusively. However, although most of these conclusions are only inferences, they are better than nothing and, with practice, a worker can infer the function of a structure with considerable accuracy. Two things must be remembered. First, such results are usually only rough approximations; we cannot hope, at this time, to determine the exact meaning of every minor variation in anatomical features. Second, as deductions, they are subject to error and hence the resulting conclusions regarding evolution and taxonomy are no better than the deductions on which they are based.

c) Lastly, the evolution of the character must be investigated. With a knowledge of its functional significance, one can estimate the selection forces which were operative during the evolution of the character. A knowledge of the selection forces is essential because while it is possible to outline the phylogeny of a structure without knowing the selection forces, it is impossible to understand its evolution without them. And here the important thing is the evolution, not the actual phylogeny, of the structure.

Once these aspects of a character are ascertained, it is possible to judge its taxonomic value. In general, the taxonomic value varies inversely with (a) the tightness of the control by the selection forces acting on the character, and (b) the changeability — independent origin, reversal of direction, etc. — of these selection forces. For example, if a structure is tightly bound to its selection forces, and if these selection forces have altered their direction frequently during the evolution of the group, then that structure would have little taxonomic value. Statements such as "the taxonomic value of a character depends upon how constant that character is within the group" are misleading and inconclusive. Lastly, I would like to suggest that the importance placed on the taxonomic value of a character be de-emphasized and that more stress be placed on studying its evolution. The former has not produced any really concrete results while the latter holds much promise for future studies of avian classification.

Before proceeding to the main part of the study, a word must be said about the classification and linear sequence of the passerine birds. The past lack of interest in the anatomy of the perching birds has resulted in chaos. In recent years, a number of conflicting classifications for the passerine families have been

proposed (Mayr and Amadon, 1951; Wetmore, 1951; Mayr and Greenway, 1956; Wetmore, 1957; Amadon, 1957; Delacour and Vaurie, 1957; and Mayr, 1958), yet these proposals and suggestions represent little more than personal opinion — the necessary information to verify the relationships suggested in these proposals does not exist. The central problem of passerine classification is the lack of factual evidence with which we can determine the evolution of the Passeres and eventually establish the most reasonable classification for them. Speculation on these problems is premature at the present time and it seems probable that it will be many years before enough information on the anatomy, behavior and other attributes of the passerines has been gathered to allow us to speculate on their phylogeny and relationships. Until that time comes, it is most advantageous to have a standard sequence of families which everyone knows and can use. For the purposes of this paper, I shall adopt the sequence agreed upon by the committee appointed by the XIth International Ornithological Congress at Basel which is the one to be used in the coming volumes of "Peters' Check-list" (Mayr and Greenway, 1956). This sequence covers only the Oscines. For the suboscines, I shall follow the sequence suggested by Wetmore (1951). I must emphasize that I do not believe that these particular systems are correct or even satisfactory. Nor do my findings support them better than the others. Nevertheless, it is strongly urged that workers in passerine anatomy follow the "Peters'" sequence until enough evidence has been gathered to establish a classification acceptable to most workers.

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anatomical feature that is not uniform throughout the order would be equally suitable for a study of this type.

It may occur in any one of four conditions — fused, unfused, free, or lateral flange.

Fused palatine process. In a typical passerine bird, such as a crow (*Corvus*, Fig. 1), we find the simplest possible adult condition of the palatine process of the premaxilla — namely, that it is lacking as a distinct structure. The anterior bars of the palatine (prepalatines or prepalatine processes) merge into the premaxillary mass without the slightest indication of a break. There are no sutures or processes at the junction of the prepalatine process and the premaxilla to reveal the presence of a palatine process of the premaxilla. The palatine process has fused completely with the prepalatine process, as will be shown later in the section on development. On the lateral side of the skull, the premaxilla merges with the maxilla, which in turn continues into the jugal bar.¹ The maxillo-palatines (not to be confused with the “palato-maxillaries”) originate from the maxillae and pass medially beneath the palatines to approach one another in the region of the anterior end of the vomer. The distal ends of the maxillo-palatines expand to form flat plates; these plates partly cover the tip of the vomer when the ventral aspect of the palate is examined. Returning to the palatines, these bones run posteriorly and then expand medially to approach the midline. The palatine shelf² and the posterior extension of the palatines (the transpalatine process) serve as the point of origin for a large part of the *M. pterygoideus* (at least for the lateral parts of this muscle). The medial parts of the palatine (the interpalatine process, anteriorly, and the mediopalatine process, posteriorly),

¹ In his recent paper on the development of the chick skull, Jollie (1957) suggests that the names for a number of bones in the skull be changed to agree with their embryological origins and homologues in the reptilian skull. Thus, for example, the palatine would become the pterygopalatine and the pterygoid would become the posteropterygoid. These new names are certainly correct technically, but the change to them would not lead to greater clarity. The technically correct names are only necessary for comparisons of the avian skull with the skull of other classes of vertebrates; however, only a very few workers are interested in this problem. The terminology used currently for the parts of the avian skull was developed specifically for the adult skull, and in many cases the term refers to a functional region or unit rather than to an individual bone. The present system of names is perfectly suitable for studies in which the skull is compared within birds. Consequently, it is recommended that the standard terminology for the parts of the avian skull be retained. I do not, however, want to convey the impression that the embryological origin of the bones of the skull is unimportant. These studies are very important and indeed, many more studies similar to Jollie's investigation of the chick skull are needed.

² The medial projection of the palatine appears to be unnamed although all of the other parts of this bone have been given special names. Because of the complex structure of the *M. pterygoideus* which originates from the palatine bone, it would be helpful if this projection also had a specific name. The most appropriate name is the medial shelf of the palatine or more simply, the palatine shelf.

the vomer and the pterygoid are of no interest to us as they are far removed from the palatine process of the premaxilla and from the muscles which may originate from it.

The fused condition of the palatine process of the premaxilla is typical for many families of passerine birds. There may be considerable variation in the relative lengths of the different processes of the palatine, but although this is of considerable importance in studies on the kinetics and functional significance of the avian skull, it is of no concern to us in this study.

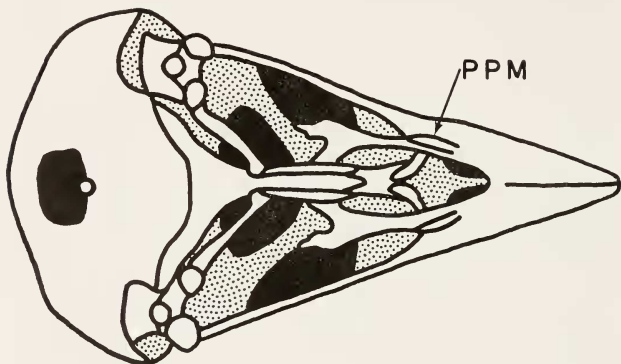


Figure 2. Ventral surface of the skull of a white-throated sparrow (*Zonotrichia*). The palatine process of the premaxilla lies along the prepalatine process of the palatine and is separated from it by a distinct suture.

Unfused palatine process. This condition of the process (called the "palato-maxillaries" by Parker, 1877, and more recently by Tordoff, (1954a, see page 374) is present in the adult stage of many genera, such as the white throated sparrow (*Zonotrichia*, Fig. 2), as a small posterior extension of the premaxilla which lies along the lateral posterior edge of the prepalatine process of the palatine. The palatine and other bones of the skull in the white throated sparrow are similar to those of the crow and need not be described again.

There is considerable variation in the length of the palatine process and in the degree of fusion between it and the palatine in the genera possessing an unfused palatine process. Some of

this variation is a result of a difference in the age of the specimens and hence in the degree of ossification of the skull; this feature of age variation will be discussed later. In some genera, the anterior end of the palatine process degenerates, thereby destroying the connection between it and the main body of the premaxilla; the final result is an isolated splint of bone lying along the lateral edge of the prepalatine process. This isolated splint of bone may appear as if it were a new bone arising from a distinct center of ossification, but it is actually nothing more than the posterior end of the palatine process detached from

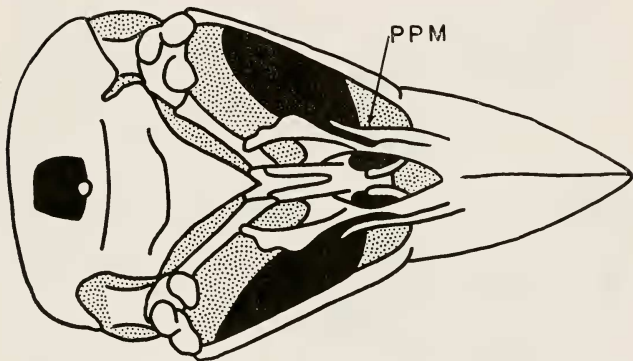


Figure 3. Ventral surface of the skull of a cardinal (*Cardinalis*). The palatine process of the premaxilla is free of the prepalatine process of the palatine and lies free in the space between the palate and the jugal bar.

the rest of the premaxilla; again, a full discussion of the development of this variant will be presented below in the section on development.

The fused condition of the palatine process may be combined with the unfused under the heading of the "normal palatine process," as found in most passerine birds.

Free palatine process. The palatine process in some groups of finches, such as the cardinal (*Cardinalis*, Fig. 3), is free of the palatine bone and lies in the space between the palate and the jugal bar. The free palatine process originates at the junction between the palatine bone and the body of the premaxilla. In some genera, there is a "suture" at the base of the free palatine process separating it from the rest of the premaxilla;

in others the palatine process continues into the rest of the premaxilla without a break (compare Figs. 31B and 31C; see also Tordoff, 1954a). The palatine and other bones of the skull are similar to those of the crow and do not require a separate description.

Lateral flange. The palatine process is lacking as a distinct structure in several groups of finches, such as the evening grosbeak (*Hesperiphona*, Fig. 4). However, in contrast to the last three types, there is a lateral flange on the anterior end of the palatine which extends almost to the jugal bar. This lateral

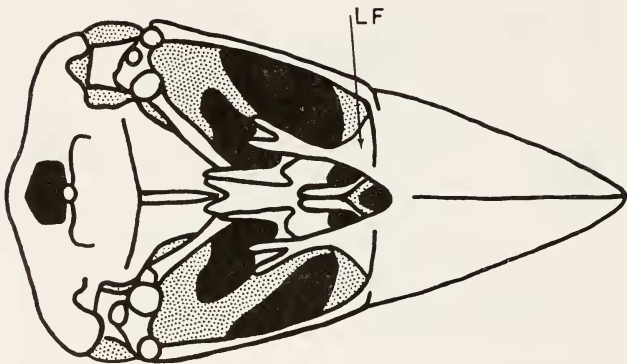


Figure 4. Ventral surface of the skull of an evening grosbeak (*Hesperiphona*). The palatine process of the premaxilla is absent (= fused to the prepalatine process of the palatine). A lateral flange is present at the site of the fused palatine process.

flange is the bony boss referred to below in the section on function and elsewhere in this paper. The lateral flange of the palatine is usually fused to the premaxillary mass, but it is sometimes separated from that bone by a suture. The palatine and other bones of the skull are similar to those described for the crow except that they are stouter and the transpalatine process is divided into two subprocesses. There is no evidence of a strengthening of "twisted" prepalatine bars such as described by Tordoff (1954a, p. 18).

HISTORY

Many of the current problems in understanding the palatine process of the premaxilla have a historical basis and thus can be fully appreciated only after one knows the history of the studies on this structure. The most important of these problems concerns the "distinction" between the palatine process and the "palato-maxillary" of Parker and of Tordoff; these terms actually refer to the same structure as will be shown below (see p. 381).

Study of the palatine process in birds began in the 1860's with the work of W. K. Parker. No other student of avian anatomy mentioned the process prior to the late 1880's. Parker clearly described and figured the palatine process of the premaxilla in all of his works including those on the palate of the "aegithognathous birds" (1875c, 1877). But, for some inexplicable reason, he stated in the description of *Tanagra cyanoptera* (1877, pp. 252-253) that: "the praemaxillary mass is . . . ; the palatine processes are aborted (*d.*, *px.*, *ppx.*).

"Where the latter processes existed in the embryo, a falcate spicule of bone appears, a separate 'palato-maxillary (*p. mx.*).' This is a character to be found in several families of the Coracomorphae, as I shall soon show. Its presence suggests some delicate bond of affinity between the families where it is found." Parker then described a "palato-maxillary" instead of a palatine process of the premaxillary in the members of the New World nine-primaried oscines. The most puzzling aspect of the "palato-maxillary" is that it appears to be identical to the palatine process of the premaxilla found in other passerine families when the two structures are compared in the adult. Yet Parker never stated how one distinguished between the two bones in the adult passerine bird. Nor did he present in this paper (1877) or in any other, the evidence supporting his belief that the palatine process aborts in the embryo of the New World nine-primaried oscines and that a separate center of ossification — the "palato-maxillary" — develops to take its place. Although Parker had studied the development of the palate in many species of passerine birds, he never investigated fully the embryology of the palate in any member of the nine-primaried complex. His only mention of the development of the "palato-maxillary" is a description of one stage in the development of the skull of a cardinal. In this description, Parker said only that the "palato-maxillaries" grow in the space between the palate and the jugal bar as additional wedges (Fig. 8A). However, he did not give the age of this

specimen, nor did he have a series of specimens of different ages; hence there is no direct evidence of the palatine process aborting and a separate "palato-maxillary" taking its place. Parker did offer a very important suggestion on a possible origin of the "palato-maxillaries" in a footnote (1877, p. 263), although he did not follow it up: "The rapid development and early ankylosis of the bony centres in birds makes the study of their osteology very difficult; also the breaking off of a projection of a primary centre to make a new bone, as in the mesopterygoid. I am in some doubt whether this lateral piece of the tetramerous vomer of the type now being described is not formed in this way. Perhaps, also, in some cases, the distinct 'palato-maxillaries' may be the palatine process of the praemaxillary detached; I have, however, no proof of this; and that process is very apt to become absorbed when no palato-maxillary appears. It is sure to be removed if a new centre came in behind it to take its place." The evidence and reasoning presented here by Parker is as strong an argument for the "palato-maxillary" being the same as the palatine process as it is for the two bones being different structures. Thus it can only be concluded that Parker did not have any good evidence supporting his belief that the palatine process of the premaxilla aborts in the New World nine-primaried oscines and that a separate "palato-maxillary" takes its place. It is difficult to understand how a worker of Parker's caliber could describe a separate bone on such flimsy evidence until one realizes that he was the first worker to describe the minute processes found in the passerine skull. In his work on the development of the palate, he had only the crudest technical aids, especially stains, and could easily be misled by a poorly preserved specimen in which the posterior tip of the palatine process had broken off and resembled a separate center of ossification. The remarkable thing is that Parker was able to describe as much as he did with primitive methods and equipment.

At this point, Parker's work on the skull of the woodpeckers (1875a) should be mentioned because he described a separate "palato-maxillary" in this group, this being the first description of the structure. According to Parker, the palatine process of the premaxilla in the woodpeckers lies on the inside of the palatine and becomes fused to the medial side of that bone, not to the lateral side as in most birds. In some (all?) species of woodpeckers, there is a separate spicule of bone lying along the lateral edge of the prepalatine process, which Parker called

the "palato-maxillary." Thus if Parker's observations are correct (I have not been able to check them), there is a separate "palato-maxillary" in the woodpeckers and the term "palato-maxillary" should be used only for this structure.

Curiously enough, later workers used only the term "palato-maxillary" even when discussing the non-New World nine-primaried passerines, and extended its meaning until it became almost synonymous with the palatine process of the premaxilla. The reason for the initial confusion is obscure, but the results are clear enough — today it is impossible to determine what is meant when the term "palato-maxillary" is used.

In the years following Parker's work, the palates of a number of passerine species were described by various workers (Garrod, 1872, 1877; Forbes, 1880, 1881, 1882; and Pyecraft, 1905a, 1905b, 1905c, 1907). Unfortunately, there is no indication whether these workers knew Parker's papers so that we can never be certain if the palatine process of the premaxilla was truly absent in the adult of the species described when an author failed to mention or to figure it; often the palatine process was overlooked if present, or otherwise omitted from discussion.

A number of workers did, however, describe the palatine process under several different names. Thus, Shufeldt (1888), in describing the osteology of *Pheucticus melanocephalus*, the black-headed grosbeak, stated (p. 439): "... the palatines on either side develop a *secondary palatine* process (sp. p., Fig. 1), extending backwards from a point to the outer side of where the anterior palatine limb fuses with the premaxillary." Later in the same paper (p. 441), he described the secondary palatine process in *Piranga* and claimed that the possession of a secondary palatine process by these birds (a tanager and a cardinaline finch) indicated an affinity between them. Apparently, Shufeldt had not seen Parker's paper on the palate of "aegithognathous birds" because his secondary palatine process is the same as Parker's "palato-maxillary." Nevertheless, the two authors agree as to the taxonomic value of this structure.

Lucas, in a series of papers (1888 to 1895), reported on the osteology of many groups of American Passeres. He did not mention the palatine process in his studies on the thrushes, the thrashers and the wrens, families in which the palatine process is usually lacking in the adult. We can be certain that Lucas had read Parker's papers for he described the palatine process (under the name "palato-maxillary") in some members of the New World nine-primaried oscines. He was, however, doubtful of its

embryological origin for he stated in his study on the osteology of the swallow-tanager (*Tersina*) (1895, pp. 505-506) that: "There is a stout palato-maxillary process, whether or not developed from a separate center is not known." In addition, Lucas questioned its taxonomic value and stated (1894, p. 304): "Its exact [taxonomic] value remains to be shown, for it appears in forms which are not related, at least closely and drops out in some that are nearly allied. It is present in the Swallows, but not in the Flycatchers or Thrushes, is well developed in such stout-billed Finches as *Cardinalis* and *Habia*, missing in *Coccothraustes*. It appears as a slender splint in *Plectrophanes* and *Calcarius*, while it is lacking in *Phoenicophilus*. None of the Drepanididae and Meliphagidae examined have a palato-maxillary." These questions posed by Lucas on the embryological origin and on the taxonomic value of the palatine process of the premaxilla, or the "palato-maxillary" as he called it, are most pertinent and have remained unanswered to the present day.

In the years between 1900 and 1950, several workers described the palatine process in a number of passerine families (Clark, 1912, 1913a, 1913b, 1913c; Lowe, 1924, 1931, 1938a, 1938b, 1947, 1949; Stonor, 1942; Sushkin, 1924, 1925, 1927, 1929), but no further contributions were made regarding its origin or taxonomic significance. Amadon, in his monograph on the Drepaniidae (1950a), included a long discussion on the "palato-maxillaries" (pp. 213-216). He stated that they are absent in the Drepaniidae, but suggested (p. 216) that the flange on the lateral side of the prepalatine bar may represent the fused "palato-maxillary." However, because of the scope of his paper, Amadon was forced to leave many questions unanswered and concluded (p. 216) that: "Little is known of the significance of the palato-maxillaries."

Tordoff's studies (1954a, 1954b) on the relationships of the "Fringillidae" and the New World nine-primaried oscines are based almost entirely on the structure and variation of the "palato-maxillaries" in these families. This work has been, up to the present, the most extensive study of the "palato-maxillaries" in any group of passerine birds and the only one that bases important taxonomic conclusions on them. Unfortunately, Tordoff did not examine families outside of the nine-primaried complex and the ploceids for the presence of "palato-maxillaries," nor did he examine the embryology of this structure. He was apparently unaware that Parker had described a very similar structure under the name "palatine process of the

premaxilla" in other passerine families and had even suggested that the two bones might be the same. In addition, Tordoff's conclusions of the functional significance of the "palato-maxillaries" are decidedly different from those arrived at in this paper. Due to the evidence presented in this study, I am unable to accept Tordoff's paper.

Recently, Jollie (1958, pp. 27-28) investigated the development of the "palato-maxillaries" in connection with his studies on the embryology of the avian skull. He showed that the "palato-maxillary" is the remnant (posterior part) of the palatine process of the premaxilla and not a separate center of ossification. This is a most important contribution to the clarification of the origin of the "palato-maxillary." Unfortunately, Jollie neglected to include a clear statement as to whether the term "palato-maxillary" is or is not synonymous with the palatine process of the premaxilla.

From this brief history of the past studies on the palatine process of the premaxilla (or the "palato-maxillary" as it is usually, but erroneously called), it can be seen that the available information is very limited in spite of the fact that it was described many years ago and has been studied by many workers. Therefore, it will be necessary to investigate all facets of the palatine process before its value in showing relationships within the Passeres can be ascertained.

DEVELOPMENT OF THE PALATINE PROCESS OF THE PREMAXILLA

The development of the palatine process must be known before several questions on its nature and identity with the "palato-maxillary" can be answered. Unfortunately, there are too few studies on the development of the skull in passerine birds and even fewer which include the development of the minor processes of the upper jaw and of the palate. The present discussion, consequently, rests almost entirely on the old but excellent studies by Parker (1872; 1873a, 1873b, and 1875b) and on the recent work by Jollie (1957 and 1958). The original contributions of the present study are meager and include only the development of the palatine process in the cardinal (*Cardinalis*), and observations on the ossification of the skull in such post-fledgling birds as are available in collections.

The following questions should be kept in mind while reading the descriptions of the development of the palatine process:

a) Is the palatine process present in the embryo of all passerine birds including those which do not exhibit a distinct palatine process as adults?

b) Is the "palato-maxillary" a separate center of ossification?

c) Is the free palatine process as seen in the adult cardinal homologous with the palatine process of other passerine birds, or is it an ossified tendon?

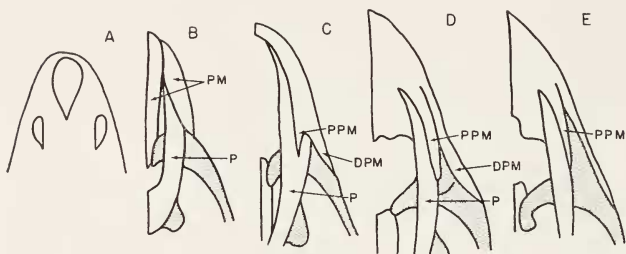


Figure 5. Series showing the development of the palatine process of the premaxilla in the crow (*Corvus*). Except for figure A which shows both halves of the skull, the figures illustrate the ventral surface of the left half of the skull. The ages of the specimens are: (A) Sixth day of incubation; (B) Ninth day of incubation; (C) Hatchling; (D) Week-old hatchling; and (E) Fledgling. The figures are redrawn from Parker (1872).

Fused palatine process. A few specimens with an unfused or a partly fused palatine process can be found in almost every large series of birds normally having the palatine process of the premaxilla completely fused with the prepalatine process in the adult (e.g., *Cyanocitta cristata*, Fig. 28F). These specimens usually show signs of immaturity, such as unossified "parietal windows." This would suggest that the palatine process is present in the young bird and becomes increasingly fused with the prepalatine process until the two bones are completely fused in the adult.

The typical course of development of the palatine process in the Passeres can be seen in the crow (*Corvus*). The following account and figures have been taken from Parker's description of the development of the skull of the crow (1872), which is still

the most complete one available for any species of passerine birds.

The premaxilla of the crow appears at about the sixth day of incubation in the form of three separate nodules of cells (Fig. 5A), the center nodule corresponding to the nasal process of the premaxilla while the lateral nodules correspond to the two halves of the main body of the bone. Neither the palatine process of the premaxilla nor the palatine have appeared by this time. By two or three days later (Fig. 5B), the nodules have enlarged and fused together to form a recognizable premaxilla. The dentary processes of the premaxilla have appeared by this time and run backwards to meet the maxillae on either side. The palatines have also appeared and are quite well developed, although the palatine processes of the premaxilla have not yet made their appearance. Parker's next stage (Fig. 5C) is a hatchling bird. The palatine processes have appeared and are small projections on the medial side of the premaxilla. They overlie the palatines. By the time the hatchling is a week old (Fig. 5D), the palatine process has enlarged to cover the lateral half of the prepalatine process. Up to the time of fledging, the palatine process continues to grow and to remain distinct from the prepalatine process (Fig. 5E). From the time of fledging or shortly thereafter, the palatine process of the premaxilla starts to fuse with the prepalatine process of the palatine until the two bones are completely fused together. There was no sign of a palatine process of the premaxilla in any of the adult crow skulls that I examined.

Among other birds possessing a fused palatine process, information on its development is available for the titmouse (Fig. 6A), the thrushes (Figs. 6B, 6C, and 6D), and the house sparrow (Fig. 7A). These species agree with the crow in possessing a distinct palatine process of the premaxilla in the embryo which becomes fused with the prepalatine process during development. The presence of a palatine process in the house sparrow (a ploceid finch) is of interest since Tordoff claimed that this group lacked "palato-maxillaries."

Unfused palatine process. The unfused condition of the palatine process, or the isolated splint lying along the prepalatine process, as seen in some of the emberizine finches, is the typical "palato-maxillary" of Parker and of Tordoff. According to Parker, the palatine process of the premaxilla aborts in the New World nine-primaried oscines and a separate center of

ossification — the “palato-maxillary” — takes its place. However, Jollie’s description of the junco, an emberizine finch (Fig. 7D) shows that the development of the palatine process in this species is identical to that described for the crow except that the fusion between the palatine process and the prepalatine process does not go to completion. I have examined a fledgling towhee (*Pipilo*) which has a perfectly normal development of the palatine process similar in all respects to that seen in the junco. Thus there is no evidence supporting Parker’s hypothesis that a separate center of ossification takes the place of the aborted palatine process.

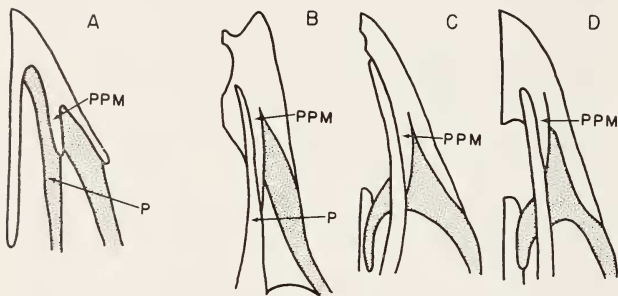


Figure 6. Development of the palatine process of the premaxilla in the titmouse (*Parus*) and the thrush (*Turdus*). Figure A shows the palatine process in a titmouse at about the tenth day of incubation; redrawn from Parker (1873a). Figures B, C, and D illustrate the palatine process in a pre-hatching *Turdus viscivorus*, a day-old *T. merula*, and a week-old *T. merula* respectively; redrawn from Parker (1873b).

The isolated splint lying along the prepalatine, which some workers might consider to be the true “palato-maxillary,” develops by the degeneration of the anterior end of the palatine process which thereby destroys the connection between the rest of the palatine process and the main body of the premaxilla. Jollie illustrates the development of this splint in the junco and I have seen good series of this change in *Formicarius* (Figs. 23D, 23E), *Spizicos* (Figs. 24D, 24E, 24F), *Melospiza* (Figs. 25G, 25H, 25I) and *Paradisaea* (Figs. 28G, 28H, 28I). These observations substantiate Parker’s hypothesis that the “palato-maxillary” may be the posterior part of the palatine process

detached from the rest of the premaxillary, and hence not a separate bone.

Free palatine process. The palatine process of the cardinal is, in many respects reminiscent of an ossified tendon. The *M. pterygoideus ventralis lateralis* originates from this process by means of a tendon, and consequently, it is possible that the entire free process seen in the cardinal could be an ossified tendon which originates from the main body of the premaxilla. My suspicions of this possibility were increased by the presence in

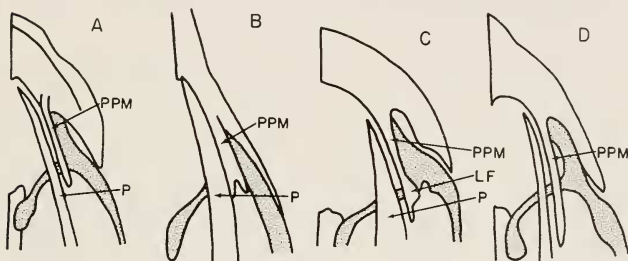


Figure 7. The palatine process of the premaxilla in: (A) A nestling house sparrow (*Passer*, redrawn from Jollie, 1958); (B) A five-day old embryo linnet (*Carduelis*, redrawn from Parker, 1875b); (C) A nestling house finch (*Carpodacus*, redrawn from Jollie, 1958); and (D) A fledgling junco (*Junco*, redrawn from Jollie, 1958).

one specimen of a faint longitudinal suture on the lateral half of the prepalatine process. This could be the suture between the semifused palatine process and the palatine if the free process seen in the adult cardinal was not the true palatine process of the premaxilla. Histological sections were prepared of the free process in the hope of ascertaining its identity. No difference could be detected between the bone of the free process and that of the premaxilla, but this result is inconclusive. Ossified tendon and bone are almost identical, if not identical, histologically. Therefore the only means of solving this problem was to study the development of the palatine process in the cardinal. Unfortunately, Parker did not give sufficient detail in his treatment on the embryology of the palate in the cardinal (see Fig. 8A) so that a series of cardinals ranging in age from hatchling to post-fledgling were gathered and stained to show the details in the

development of the palatine process. These specimens (Figs. 8B, 8C, 8D) prove that the free process in the cardinal is the true palatine process of the premaxilla and not an ossified tendon. It is possible that the tendon attaching to the free process has ossified for a short distance starting at its origin and thus has elongated the process, but this would be exceedingly difficult to verify. However, even if the free process was enlarged through ossification of the attached tendon, it would still be the palatine process. The position of the palatine process in a hatchling rose-breasted grosbeak (*Phœucticus*) also indicates that the free process in this species is the true palatine process of the premaxilla.

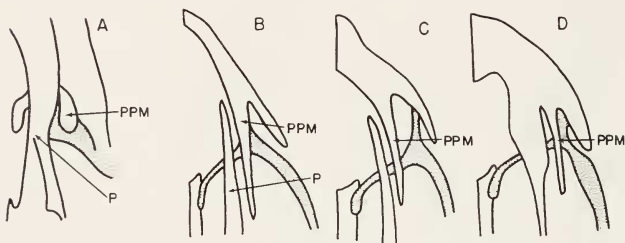


Figure 8. Development of the palatine process of the premaxilla in the cardinal (*Cardinalis*). Figure A is a bird of unknown age redrawn from Parker, 1875b. The series B, C, and D are drawn from specimens of a hatchling cardinal, a fledgling cardinal, and a post-fledgling, half-grown cardinal, respectively.

Lateral flange. Those birds, such as the cardueline finches, which possess a lateral flange at the anterior end of the palatine, also lack a palatine process in the adult. Tordoff stated that the Carduelinae do not have a "palato-maxillary" (with the tacit assumption that it is also absent in the embryo) and are therefore related to the ploceid finches. However, Parker (1875b) shows a very distinct palatine process in the early embryo (five days) of the linnet (Fig. 7B) and Jollie (1958, p. 29) shows an equally distinct process in the house finch (Fig. 7C). Hence, the palatine process of the premaxilla is present in the embryo of the cardueline finches and becomes fused to the palatine during development. Ossification of the lateral flange starts at the palatine process as can be seen in Jollie's figure of the house finch (Fig. 7C).

Conclusion. The palatine process of the premaxilla is present in the immature of all studied species of passerine birds and it is probably present in the immature of all passerines (see also, Jollie, 1958, p. 27, who concludes that the palatine process is probably present in the immature of all birds). It is most probable that the palatine process was overlooked in those studies (e.g., Huggins, *et al.*, 1942) in which it is not mentioned. In most passerines, the palatine process becomes indistinguishably fused with the prepalatine process of the palatine during post-hatching development. There is no indication of the palatine process aborting and a separate center of ossification taking its place in the New World nine-primaried oscines. Therefore, all of the structures in the passerine birds which have been called the "palato-maxillary" or the "secondary palatine process" are the same as the palatine process of the premaxilla; that is, these terms are synonymous. None of these structures, e.g., the free process in the cardinals, are non-homologous structures which have been misidentified as the palatine process. Lastly, it is best not to give the isolated splint lying along the prepalatine process a separate name. This procedure implies that the splint developed as a separate bone while it is nothing more than the posterior part of the palatine process detached from the main mass of the premaxilla.

FUNCTION OF THE PALATINE PROCESS OF THE PREMAXILLA

Analysis of the functional significance of most morphological systems is, by necessity, based on deductive reasoning. The functional conclusions are only hypotheses and must be treated as such. Only after these hypotheses have been tested by extensive experiments, can they be relied upon and, even then, there is a chance that some important factor has been overlooked. The deductive method of functional anatomy is based partly on a consideration of the laws of mechanics and partly on a consideration of the relative development of the structure in forms having different habits. For instance, if the shape and mass of certain jaw muscles differ between seed-eating and insect-eating birds, then the basic assumption would be that this difference is somehow associated with feeding habits. The details of the particular functions are, then, worked out using the principles of mechanics. This simple method has enabled functional anatomists to analyze highly complex systems, even though their

results are largely hypothetical. It is hoped that experimental workers will test the conclusions of functional anatomy and determine which of their conclusions and working hypotheses are correct. Such work may be most difficult from a technical standpoint, but the results would be invaluable to students of anatomy and evolution.

The palatine process of the premaxilla has three major functions which are partly independent of one another. One function is found in all passerine birds and is complementary to the two others which appear to be mutually exclusive. The first function is the insurance of a firm connection between the palate and the upper jaw, while the two mutually exclusive ones are: a point of origin for part of the *M. pterygoideus*, and a bony boss against which seeds are crushed. The first function may be considered to be the primary function of the palatine process and the others to be secondary ones. This division of functions into primary and secondary ones is not to be confused with original and successive functions; it is a division according to relative importance, not according to the time of appearance. A function may be defined as primary if it is the most important or the most basic function of the structure. It is present in all species possessing the structure and thus can be considered as the function responsible for the maintenance or the preservation of the structure. Secondary functions are subservient to the primary function in that their action must be in harmony with the action of the primary function. Usually secondary functions are not found in all species possessing the structure. An example of primary and secondary functions may be found in the avian wing. Active flight is generally the primary function of the wing, while display, defense, underwater swimming and so forth are secondary functions. So long as a bird must be able to fly, these secondary functions are subservient to the primary function of flight. Although the primary function is responsible for maintaining a structure, it is not necessarily responsible for the origin of that structure. A former secondary function could have become the primary function in the course of evolution and thus become responsible for the preservation of the structure. The original primary function would then become a secondary function or drop out entirely. This is the well-known phenomenon of preadaptation or functional change (*Funktionwechsel* of Dohrn, see Bock, 1959). In the example of the avian wing, active flight is currently the primary function, but it is not the original function responsible for the origin of the wing. The original function was

probably gliding which was replaced by active flight when the fore limb became sufficiently developed as a wing to acquire this new function. Similarly, underwater swimming was once a secondary function of the wing in the ancestral penguins, as it is in the auks and the diving-petrels, but became the primary functions when penguins no longer needed to fly.

The following analysis will be divided into two parts. The first will deal with the function responsible for maintaining the palatine process in birds, while the second will deal with the functions responsible for the modifications of the process during the evolution of the Passeres. Throughout the discussion, I will switch from the function to the selection force associated with that function and vice versa. In general, there is a major selection force for each function and that selection force can be described in the same terms as the function. Thus, if the function of a bony process is that of a brace to support the bone, then the selection force is for a brace to support the bone. For those who are not used to switching from function to selection force, the best way to keep the two separate is to think of the function as the static phenomenon and the selection force as the dynamic phenomenon.

Before proceeding to the discussion of the function of the palatine process, it is necessary to establish the limits of this study. The palatine process of the premaxilla is part of the extensive character complex of bones, muscles, ligaments and other structures that make up the jaw mechanism. A character complex may be defined as that group of characters that acts together as a single functional unit. A structure may belong to several character complexes, and a large complex, such as the jaw mechanism, may be divided into a number of smaller component complexes. Whenever possible, the entire character complex, not the individual component characters, should be the unit of study. A complete study of the jaw mechanism in the Passeres is most desirable and must eventually be done in order to understand the passerine feeding modifications and the relationships between groups of passerine birds (e.g., the development of the seed-cracking bill versus the relationships between the various groups of finches), but I do not have the knowledge to undertake such a study at this time. In this paper, I have restricted myself to the function of the palatine process of the premaxilla, but have included the function of such other structures as seemed pertinent to the problem.

Maintenance of the palatine process. The kinetic skull of birds with its movable upper jaw necessitates a firm connection between the palate and the upper jaw. The strength of this connection is increased by the palatine process which provides a larger surface to which the palatine can fuse. Hence, it is postulated that the primary function of the palatine process is to insure a firm connection between the palate and the upper jaw, and that the selection force associated with this function would be for a stronger connection between the palate and the upper jaw. A discussion of the mechanics of the skull can provide some

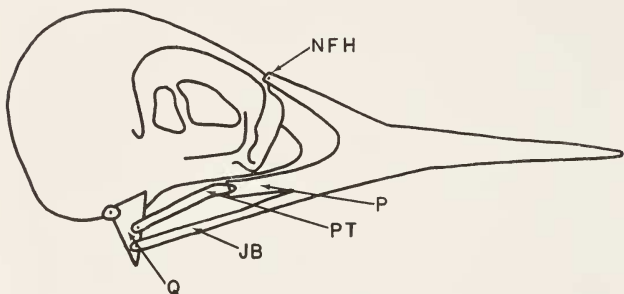


Figure 9. Diagrammatic drawing showing the mechanics of the kinetic skull in birds. When the quadrate rocks forward, it pushes on the jugal bar and the palate which in turn push on the base of the upper jaw. Because it is attached to the braincase at the nasal-frontal hinge, the upper jaw rotates upward. When the quadrate rocks backwards, the upper jaw rotates downward. Redrawn from Engels, 1940.

evidence supporting this hypothesis. I will only outline the salient features of this mechanism and refer the interested reader to Beecher's excellent discussion of the mechanics involved in elevating and depressing the upper jaw in birds (1951a, pp. 412-416).

The upper jaw of birds is not solidly fused to the braincase as in mammals and in some reptiles, but can be raised and lowered by means of a complex mechanism of bones (Fig. 9). Rotation of the upper jaw is about the nasal-frontal hinge — the connection between the upper jaw and the braincase. At its ventro-posterior end, the upper jaw is attached to the jugal bars laterally and to the palate medially. These elements connect the upper

jaw to the quadrate. All parts of this system except for the nasal-frontal hinge are free of the braincase and can move relative to it. Thus, as the quadrate rocks forward, it pushes the base of the upper jaw forward. The upper jaw, being attached to the braincase at the nasal-frontal hinge, rotates upward (Fig. 10). When the quadrate rocks backwards, it pulls the base of the upper jaw backwards and thus depresses the upper jaw. Because the muscles operating this system insert on the quadrate and the pterygoid, their force must be transmitted to the upper jaw by means of the palate and the jugal bars. The push that raises the upper jaw is probably transmitted to it only through the palate because the thin jugal bars would bend if a push was exerted on them. The pull could be transmitted through the palate and the jugal bars; however, it seems likely that most of the pull is along the palate. Hence, in addition to other factors, the proper functioning of this kinetic system is dependent upon a strong connection between the palatines and the premaxilla.

At least two important functions are achieved by the kinetic skull of birds. First, it permits a wider gape than a stationary upper jaw; this feature is desirable in such birds as the swallows and the flycatchers, which need a wide gape. Second, it preserves the primary orientation of the skull (see Moller, 1931, p. 146; Beecher, 1951a, pp. 414-415) by allowing the bird to open its bill without shifting the position of the eye with reference to the prey or "leading" the prey (Fig. 10). If the axis of the skull shifted when the bird opened its bill to capture its prey, the entire orientation of the head and neck in respect to the prey would be destroyed. The bird would have to re-orient completely in the brief instant between bill-opening and prey-capture. Development of the elaborate nervous mechanism needed for this rapid re-orientation would be difficult. It would be far easier to preserve the orientation of the skull by mechanical means, e.g., a kinetic skull. Evolution in birds has followed the latter course. The importance of these functions is indicated by the fact that almost all birds possess a kinetic skull. Hence there would be a strong selection force favoring all parts of the kinetic skull, including a firm connection between the upper jaw and the palate. It was postulated above that the palatine process of the premaxilla serves to increase the contact and presumably the degree of fusion between the premaxilla and the prepalatine process of the palatine; thus the palatine process would be favored by the selection force for the kinetic skull. Therefore, it can be concluded that the selection forces favoring the kinetic

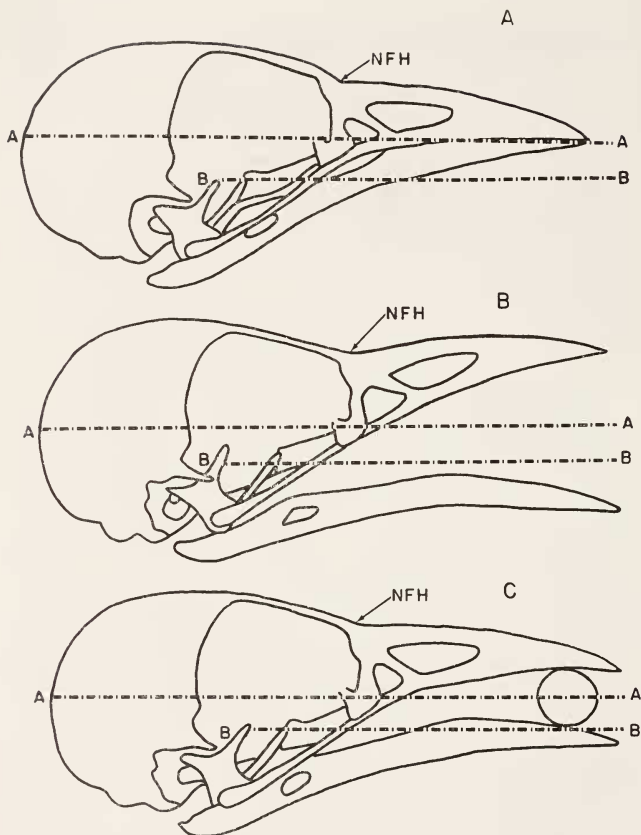


Figure 10. Diagrammatic drawings of the avian skull illustrating how the kinetic upper jaw preserves the primary axis of the skull, i.e., the position of the eyes in respect to the prey. Line A-A represents the primary axis of the skull; it lies along the gonys (the junction between the upper and lower jaws) as shown in figure A. The primary axis remains stationary and midway between the jaws when the bill opens (Figure B) and closes on the prey (Figure C). Line B-B represents the secondary axis of the skull when the bill opens if the upper jaw is not movable. Figures redrawn from Moller, 1931.

skull are responsible for maintaining the palatine process of the premaxilla in birds.

It should not be assumed that the palatine process of the premaxilla appeared as a new structure in the passerine birds. The palatine process had doubtless originated at the time birds evolved from reptiles, if not before. The palatine in most reptiles abuts against the maxilla and the vomer anteriorly and against the pterygoid posteriorly. In birds, the anterior connection of the palatine is with the premaxilla and perhaps with the maxilla by means of secondary ossification. The connection with the vomer is medial and more posterior than in the reptiles while the connection with the pterygoid is posterior as usual. The shift of the palatine from the maxilla to the premaxilla probably required the development of a point of abutment or anchorage on the premaxilla. This is the palatine process of the premaxilla. It is not known whether the shift of the palatine was associated with the development of the kinetic skull in birds because the palates of neither the pseudosuchians nor *Archaeopteryx* are known. The kinetic skull evolved sometime after the *Archaeopteryx*-stage in the evolution of birds. Nevertheless, once birds possessed a kinetic skull and a palatine process of the premaxilla, the palatine process was preserved because of the selection forces associated with the kinetic skull. It was thus available (preadapted) for other selection forces which arose during the subsequent evolution of the passerine birds.

Modifications of the palatine process. Modifications in the structure of the palatine process of the premaxilla in the Passeres have developed under the control of the several secondary functions of this structure. These will be discussed with three problems in mind. (a) Changes in the palatine process associated with modifications in the M. pterygoideus. These changes arose in connection with the development of a free palatine process, such as is found in the cardinal. (b) Development of a bony boss at the anterior end of the palatine. This is associated with the development of the lateral flange on the anterior end of the palatine in the cardueline and other finches. (c) The variation in the degree of fusion between the palatine process of the premaxilla and the palatine, and the variation in the development of the isolated splint lying along the palatines as seen in the emberizine finches.

These are not sharply separated problems, but are all inter-related under the general heading of adaptive modifications in the bill for seed-eating. I shall, therefore, first describe the

various functional mechanisms of the avian jaw which are prerequisite for understanding the modifications in the palatine process of the premaxilla and, then, under the heading of conclusions, return to these questions and answer them as best I can. Discussion of the functional mechanisms will be in the following order: first, the structure, function and variation of the *M. pterygoideus* in the Passeres; second, a comparison of the adaptive pathways through which the strength of the bite can be increased; third and last, a comparison of the jaw muscles and seed-cracking methods in the several groups of finches.

The M. pterygoideus. Tordoff (1954a, p. 12) assumed that the origin and evolution of the palatine process of the premaxilla (his "palato-maxillary") was dependent upon changes in the mass of the *M. pterygoideus*. However, he apparently only examined the jaw muscles of the cardinal (*Cardinalis*) and extrapolated the correlation between the palatine process and the *M. pterygoideus* in the other New World nine-primaried oscines from the condition seen in the cardinal. To be sure, part of the *M. pterygoideus* originates from the palatine process in the cardinal, yet it is necessary to survey the jaw musculature in the Passeres and to correlate the changes in the *M. pterygoideus* with the modifications in the palatine process before any statements about the evolution of the palatine process can be made. It can be stated in advance that the *M. pterygoideus* is the only jaw muscle that originates from the palatine process of the premaxilla.

Dissection of the *M. pterygoideus* is rather difficult because of the incomplete separation of the muscle into four parts and the complex arrangement of the muscle fibers. Much care must be taken to separate the parts correctly and to determine the direction of the muscle fibers in each part. The *M. pterygoideus* is usually divided into a ventral and a dorsal portion and each portion is, in turn, divided into a lateral and a medial half (Lakjer, 1926, pp. 65-67). Some workers (e.g. Engels, 1940, pp. 359-361) do not recognize any subdivisions of the *M. pterygoideus* because they cannot separate the parts with complete certainty. It is true that the subdivisions of the *M. pterygoideus* are not clearly defined units, but it is not necessary for the parts of a muscle to be sharply separated from one another before they are recognized as separate units. If the parts of a muscle, such as the *M. pterygoideus*, have different functions and are unequally developed in different forms, then they are best recognized even if they are not sharply separated from one another. It should

be emphasized that the functional unit of a muscle is not the whole muscle, or a recognizable part thereof, or even a muscle fiber, but the motor unit—which is the aggregate of muscle fibers innervated by a single nerve fiber (= motor cell axon). If we wish to be completely precise in our studies of muscle function, then we must separate the muscle into its motor units, which is an impossible task. Therefore, the degree of analytical precision is not noticeably reduced if the recognized subdivisions of a muscle merge into one another.

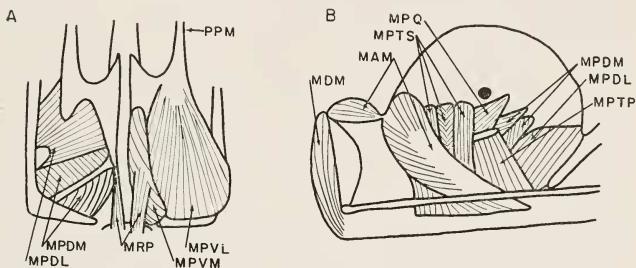


Figure 11. Jaw muscles of the gray jay (*Perisoreus canadensis*). (A) Ventral view of the M. pterygoideus. (B) Oblique view into the orbit showing the dorsal jaw muscles and the dorsal aspect of the M. pterygoideus. In the ventral view of the jaw muscles of this and all other species, the posterior end of the palatine process of the premaxilla or a point on the palatine posterior to the palatine process is indicated by an arrow (PPM). Thus the reader can note the relationship between the palatine process and the M. pterygoideus ventralis lateralis. In the gray jay, for example, there is no connection between the palatine process and the M. p. ventralis lateralis.

The following description of the M. pterygoideus (Fig. 11) is for the gray jay (*Perisoreus canadensis*), a bird having a medium-sized bill of fairly generalized shape. I shall regard the arrangement of the M. pterygoideus in this species as "typical" for the Passeres.

a) M. pterygoideus ventralis lateralis. This large segment comprises almost all of the ventral portion of the M. pterygoideus. It originates from the entire ventral surface of the transpalatine process and from much of the ventral surface of the medial shelf of the palatine, and inserts on the medial and ventral surfaces of the mandible and on the medial process of the

mandible ("internal articular process" of some authors). Both the origin and insertion of this muscle are fleshy. The *M. p. ventralis lateralis* is a fan-shaped muscle with some of its medial fibers inserting on the *M. p. ventralis medialis*. It is important to note that in the gray jay, the origin of the *M. p. ventralis lateralis* is from the transpalatine process and the medial shelf and not from the region of the fused palatine process of the premaxilla; that is, there is no association between this muscle and the palatine process. The *M. p. ventralis lateralis* is, however, the part of the *M. pterygoideus* that may take origin from the palatine process of the premaxilla in some groups of passerine birds.

b) *M. pterygoideus ventralis medialis*. This small subdivision of the *M. pterygoideus* comprises only a minor part of the ventral portion of the muscle and is frequently difficult to separate from the lateral part. It originates from the lateral side and from the tip of the mediopalatine process, and inserts on the distal end of the medial process of the mandible. Both the origin and the insertion are fleshy and the fibers are parallel to one another. Because of its position, the *M. p. ventralis medialis* is never associated with the palatine process of the premaxilla.

c) *M. pterygoideus dorsalis lateralis*. This large segment of the dorsal part of the *M. pterygoideus* lies directly over the slightly larger *M. p. ventralis lateralis*; only in some of the heavy-billed finches is the *M. p. ventralis lateralis* smaller than the *M. p. dorsalis lateralis*. It takes origin from the dorsal surface of the transpalatine process and the medial shelf of the palatine, and inserts on the medial side of the mandible just dorsal to the insertion of the *M. p. ventralis lateralis*. The muscle fibers appear to be parallel to one another and to run obliquely backwards from their origin to their insertion.¹ Except for a small aponeurosis at the corner between the mandible and its medial process, the origin and insertion of this muscle are fleshy in the gray jay; in some birds, they are quite tendinous. In the gray jay, the origin of the *M. p. dorsalis lateralis* is limited to the posterior part of the palatine and is far removed from the fused palatine process. However, in some passerine birds, the origin

¹ Actually these fibers are not parallel, but are pinnate for they insert on a membrane that runs along the dorsal side of the muscle rather than directly on the mandible. Pfuhl (1936) stresses this problem of the true pinnate nature of some apparent parallel-fibered muscles, but for simplicity I shall regard pinnate muscles of the *M. p. dorsalis lateralis* type as parallel-fibered. I realize that this is incorrect and that someday a correct description of these muscles must be given, but this simplifying assumption will not affect the results of the present paper.

of the *M. p. dorsalis lateralis* extends forward along the palatine as far as the premaxilla. In these groups, the origin of this anterior extension of the *M. p. dorsalis lateralis* is usually from the dorsal surface of the prepalatine process. But in those few groups where it takes origin from the lateral edge of the prepalatine process, the *M. p. dorsalis lateralis* is not associated with the palatine process of the premaxilla.

d) *M. pterygoideus dorsalis medialis*. This is the most sharply defined part of the *M. pterygoideus*. It takes origin from both sides of the pterygoid bone and from a small part of the posterior tip of the mediopalatine process, and inserts on the distal tip of the medial process of the mandible. The pterygoid divides this muscle into an anterior and a posterior part. The anterior fibers are pinnate, inserting on a tendon that runs along the anterior edge of the muscle; the posterior fibers are parallel. Except for the insertion of the anterior fibers, the origin and insertion of this muscle are fleshy. Because of its medial position, the *M. pterygoideus dorsalis medialis* is never associated with the palatine process of the premaxilla.

e) "*M. retractor palatini*." The "*M. retractor palatini*" is not a separate muscle as listed by some workers, but is part of the *M. pterygoideus*. In most passerine birds, some of the medial fibers of the *M. pterygoideus* run directly backward and insert on the basitemporal plate instead of on the distal tip of the medial process of the mandible. In the gray jay, a few fibers appear to take origin from the middle of the *M. p. ventralis medialis* and insert on the basitemporal plate. These fibers, which form a very thin layer of tissue in the gray jay, are homologous with a band of fibers in such groups as the thrashers and the thrushes that originate on the medial shelf of the palatine next to the *M. p. ventralis lateralis* and pass over the *M. p. ventralis medialis* to insert on the basitemporal plate. These fibers are probably part of the *M. p. ventralis medialis* although they appear to be associated with the *M. p. ventralis lateralis*. (I shall discuss this group of fibers in more detail below, p. 396). In addition to these ventral fibers, a small group of fibers run back from the posterior tip of the mediopalatine process to insert on the basitemporal plate dorsal to the insertion of the ventral fibers. The fibers that insert on the basitemporal plate may be grouped together as a part of the *M. pterygoideus* or they may be included as part of the *M. p. dorsalis medialis* or the *M. p. ventralis medialis* according to their position. I will identify them on the figures as the "*M. retractor palatini*," but will consider them as part of the medial

portion of the *M. pterygoideus* in functional discussions. The fibers of the "*M. retractor palatini*" are never associated with the palatine process because of their extreme medial position.

Function of the M. pterygoideus. The action of the *M. pterygoideus* is usually described as raising the lower jaw and lowering the upper jaw; however, this is not precise enough for the purposes of this paper. Presumably, each of the four parts of the *M. pterygoideus* has its own innervation and can contract independently of the others. Also, only one part may enlarge to meet the demands of a particular selection force. If all four parts of the *M. pterygoideus* had the same function, then one would expect that the whole muscle would evolve as a unit. Certainly then, it can be assumed that, although the action of the *M. pterygoideus* is to close the bill, the exact role of each of its four parts in closing the bill differs and must be determined. The following discussion is an attempt to ascertain the action of each part of the *M. pterygoideus* from an analysis of their origins and insertions, the directions of their muscle fibers, and their relative development in different types of birds.

The parts of the *M. pterygoideus* which serve to raise the mandible must be so oriented that their pull causes the depressed mandible to swing upward about its quadrate articulation. To envision the direction of these muscle fibers, one must consider the mandible and the *M. pterygoideus* from their lateral side as well as from their ventral side. Two groups of fibers possess the qualifications for raising the mandible. The first are those fibers originating from the lateral side of the palate, the transpalatine process and the palatine shelf and inserting on the medial side of the ventral edge of the mandible anterior to its articulation. These fibers draw the mandible directly upward and would be effective even with the bill almost closed. The second group of fibers are those which originate from the transpalatine process and the palatine shelf and insert on the medial process of the mandible, usually on its anterior face but sometimes along the ventral edge of its posterior face. These fibers pull the medial process of the mandible forward and thereby raise the mandible. When the mandible is depressed, the medial process is slightly posterior and ventral to its position when the bill is closed. The difference between the normal and the depressed position of the medial process is very small, perhaps only $\frac{1}{10}$ of the distance between the posterior tip of the transpalatine process and the medial process of the mandible when the bill is closed. This means that a slight movement of the medial process toward its

normal position results in the mandible being raised over a considerable distance. Because of their insertion near the quadrate hinge, these fibers raise the mandible rapidly, but with little power. The medial process reaches its final position when the bill is about half closed. Thus, the fibers of this second group are effective in raising the mandible only when the bill is wide open and can no longer serve in this connection after the bill is half closed. Lastly, it should be mentioned that those fibers which insert along the ventral edge of the posterior face of the medial process rotate the process and thereby raise the mandible. These fibers may be effective in raising the mandible until the bill is almost closed; however, I have not studied this point in detail.

Lowering of the upper jaw would depend upon the ability of the *M. pterygoideus* to retract the palate. Probably all of the fibers of this muscle, no matter what their origin and insertion might be, would draw the palate backward. However, those fibers which run obliquely from the palate to the medial side of the mandible exert only a slight backward pull on the palate. The fibers which retract the palate most effectively are those that originate on the posterior part of the palate and run directly back to insert on the medial process of the mandible. Those particular fibers which insert on the basitemporal plate can only retract the palate; they cannot have any effect on the mandible. Lastly, the fibers which originate from the pterygoid probably have as their only action, the lowering of the upper jaw.

With these background remarks in mind, the following actions may be suggested for the parts of the *M. pterygoideus*.

a) *M. p. ventralis lateralis*. The lateral fibers of this muscle act mainly to raise the mandible. The medial fibers, which insert on the medial process of the mandible, retract the palate and thus depress the mandible during their entire contraction cycle, but can serve to raise the mandible only when the bill is about half closed. In the insect-eaters, the *M. p. ventralis lateralis* is probably more important as a palatine retractor, but in the large-billed seed-eaters, this muscle is probably more important as an adductor of the mandible.

b) *M. p. ventralis medialis*. This muscle, by virtue of its origin on the mediopalatine process and its insertion on the distal tip of the medial process of the mandible and the basitemporal plate, has as its major and probably only action, the retraction of the palate. It may be noted that those birds which need large palate retractors, such as the swallows and the flycatchers, have a large *M. p. ventralis medialis*. I include those fibers which

originate on the palatine next to the M. p. ventralis and pass over the M. p. ventralis medialis to insert on the basitemporal plate (see drawing of the thrasher, Figs. 13A and 13B) as part of the M. p. ventralis medialis; their function is, of course, palatine retraction.

c) M. p. dorsalis lateralis. All of the fibers of this muscle run obliquely from the palatine bone to the medial side of the mandible. Thus, the action of this muscle is to raise the mandible with, at most, a very minor part of the force used to retract the palate. It could be noted that this muscle is small in insect-eaters and greatly enlarged in seed-eaters.

d) M. p. dorsalis medialis. This muscle takes origin from the pterygoid and the posterior end of the mediopalatine process and inserts on the distal end of the medial process of the mandible and the basitemporal plate; hence its sole action is retraction of the palate.

To recapitulate, the major function of the medial parts of the M. pterygoideus is to retract the palate and hence depress the upper jaw, while the major function of the lateral parts is to raise the lower jaw. The medial fibers of the M. p. ventralis lateralis can raise the mandible only during the early part of their contraction while they can retract the palate during all of their contraction. This separation of functions between parts of the M. pterygoideus is not a sharp one, for it seems likely that each part of the muscle has at least a small role in both functions. However, this division of labor between the parts of the M. pterygoideus is clearly reflected in their relative sizes in different types of passerine birds, as for example, insect-eaters as compared to seed-eaters.

Variation of the M. pterygoideus in the Passeres. The results of a survey of the M. pterygoideus in the Passeres will be reported in this section. This survey is far from complete, but it does include a number of different types of passerine birds and is, I believe, adequate for the purposes of this paper. The muscle will not be described in detail as has been done for the gray jay; instead, its ventral aspect will be figured for each species available. In the figure, the posterior end of the palatine process will be indicated to allow the reader to determine the relationship between the M. p. ventralis lateralis and the palatine process. A word of warning should be given. First, my drawings are crude representations of the very complex system of jaw muscles. I have tried to show the spatial relationships of the muscles and the directions of the fibers; however, I cannot vouch for the accuracy of the proportions or the perspective. These

figures were drawn to illustrate the points discussed in this paper and should not be used to illustrate any other aspect of the jaw muscles. Second, the style of each author differs; thus much of the difference in the jaw muscles in a bird as shown by Engels or Fiedler or myself is artificial. The significance of this survey in relation to the functional significance and evolution of the palatine process will be discussed in the conclusion of this section.

The method used in dissecting the *M. pterygoideus* was simply to remove the hyoid apparatus and associated muscles, to cut off the mandible just anterior to the insertion of the *M. pterygoideus*, and lastly to remove the lining on the roof of the mouth plus the horny covering of the upper jaw. Usually the eye was also removed to allow examination of the other jaw muscles and the dorsal aspect of the *M. pterygoideus*. The *M. pterygoideus* is now exposed and after some cleaning up of connective tissue and blood vessels, it is ready for study. Some care must be taken when removing the lining of the mouth and the horny palate to make certain that the tendons and muscle fibers in the region of the prepalatine process are not damaged or destroyed.

The following species are available for comparison:

Tyrannidae	<i>Tyrannus dominicensis</i>	Figure 12A
Alaudidae	<i>Eremophila alpestris</i>	" 12C and 12D
Hirundinidae	<i>Iridoprocne bicolor</i>	" 12B
Bombycillidae	<i>Bombycilla cedrorum</i>	" 12E
Troglodytidae	<i>Heleodytes brunneicapillus</i>	" 12F
Mimidae	<i>Toxostoma redivivum</i>	" 13A
	<i>Toxostoma rufum</i>	" 13B
	<i>Nesomimus macdonaldi</i>	" 13C
	<i>Dumetella carolinensis</i>	" 13D
Turdinae	<i>Turdus philomelos</i>	" 13E
	<i>Turdus migratorius</i>	" 13F
	<i>Hylocichla</i> sp.	" 14A
Paradoxornithinae	<i>Paradoxornis</i> sp.	" 14B
Poliophtilinae	<i>Poliophtila caerulea</i>	" 14D
Sylviinae	<i>Regulus calendula</i>	" 14C
Paridae	<i>Parus bicolor</i>	" 14E
Sittidae	<i>Sitta europaea</i>	" 14F
Nectariniidae	<i>Cinnyris chalybaeus</i>	" 15A
Zosteropidae	<i>Zosterops annulosa</i>	" 15B
Meliphagidae	<i>Anthornis melanura</i>	" 15C
Emberizinae	<i>Emberiza citrinella</i>	" 15D
	<i>Passerella iliaca</i>	" 15E and 15F
	<i>Melospiza melodia</i>	" 17A

Emberizinae (cont'd)	<i>Spizella pusilla</i>	Figure 16A and 16B
	<i>Pipilo erythrophthalmus</i>	" 16E and 16F
	<i>Zonotrichia albicollis</i>	" 16C and 16D
Cardinalinae	<i>Cardinalis cardinalis</i>	" 17E and 17F
	<i>Passerina cyanea</i>	" 17C and 17D
	<i>Piranga rubra</i>	" 17B
Tanagrinae	<i>Dacnis cayana</i>	" 19B
Coerebinae	<i>Sciurus aurocapillus</i>	" 18C and 18D
Parulidae	<i>Vireo olivaceus</i>	" 18A and 18B
Vireonidae	<i>Molothrus ater</i>	" 18E and 18F
Icteridae	<i>Quiscalus quiscula</i>	" 19A
Fringillinae	<i>Fringilla coelebs</i>	" 19C and 19D
	<i>Spinus tristis</i>	" 19E and 19F
Carduelinae	<i>Carpodacus purpureus</i>	" 20C
	<i>Hesperiphona vespertina</i>	" 20A and 20B
	<i>Carduelis carduelis</i>	" 20D
	<i>Pinicola enucleator</i>	" 20E
	<i>Loxia curvirostra</i>	" 20F
	<i>Coccothraustes coccothraustes</i>	" 21A
Estrildidae	<i>Lonchura orizivora</i>	" 21B
Ploceidae	<i>Passer domesticus</i>	" 21C and 21D
Sturnidae	<i>Sturnus vulgaris</i>	" 21E
Corvidae	<i>Corvus crassirostris</i>	" 21F
	<i>Perisoreus canadensis</i>	" 11

Some comparative notes on the structure of the M. pterygoideus can be given at this point. It has already been pointed out that, in the seed-eaters, the medial parts of this muscle are relatively small while the lateral parts are relatively large. In the insect-eaters, the medial parts are relatively large, although they are still smaller in mass than the lateral parts of the M. pterygoideus; the M. p. ventralis lateralis makes up a major share of the total mass of the muscle. For example, the M. p. dorsalis lateralis is very small in the kinglet (*Regulus*) and the gnat-catcher (*Poliophtila*), while the medial parts of the M. pterygoideus comprise only about 5 per cent of the total muscle mass in such heavy-billed finches as the evening grosbeak (*Hesperiphona*). The structure of the "M. retractor palatini" in the Old World insect-eaters, such as the kinglet, thrushes, thrashers and wrens, is very characteristic. The dorsal band of fibers originates along with the M. p. dorsalis medialis from the distal tip of the mediopalatine process, and is unquestionably part of that muscle. The ventral band of fibers originates from the palatine shelf next to the M. p. ventralis lateralis and passes over the M. p. ventralis medialis before inserting on the basitemporal plate. Although these fibers appear to be part of the

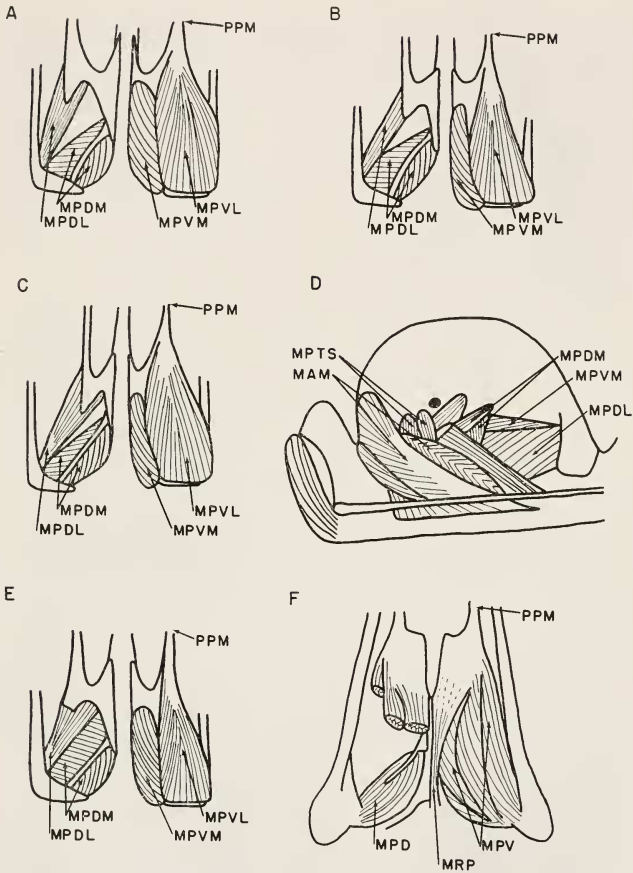


Figure 12. Jaw muscles of: (A) *Tyrannus*; (B) *Iridoprocne*; (C and D) *Eremophila*; (E) *Bombycilla*; and (F) *Heleodytes* (redrawn from Engels, 1940).

M. p. v. lateralis, they are most probably part of the M. p. v. medialis. They may have at first originated from the ventral edge of the mediopalatine process along with the rest of the M. p. v. medialis and then moved laterally to the palatine shelf as their mass increased. It is possible that these fibers are part of the M. p. v. lateralis and that their insertion shifted from the medial process of the mandible to the basitemporal plate, but this does not seem probable. A more thorough study of the innervation of these fibers is needed before we can be certain of their origin.

Beecher (1951a, 1953) illustrated the dorsal aspect of the M. pterygoideus and identified four subdivisions—the M. p. dorsalis anterior, M. p. dorsalis posterior, M. p. ventralis anterior and M. p. ventralis posterior (Beecher's terminology). Most of his figures (1953) show the usual four subdivisions, but some (sunbird, p. 291; white-eye, p. 291; wood warbler, p. 306; see Fig. 22B; and wren, p. 318) show five subdivisions (the identity of the fifth subdivision is usually not mentioned) and others show only three subdivisions. In the case of birds with only three parts of the M. pterygoideus visible through the orbit, these parts are always the M. p. d. anterior, M. p. d. posterior and the M. p. v. anterior, as for example, in the house finch, the cowbird (Fig. 22D) and the song sparrow (Fig. 22C). In the latter species, there can be no doubt of Beecher's identification of the M. p. v. anterior for he states (1953, p. 307) that: "Large M. 4a [= M. p. v. anterior] overlying M. 4b [= M. p. v. posterior]." Yet my dissections of the finches revealed that the origin of the M. p. dorsalis lateralis extended anteriorly along the prepalatine process as far as the premaxilla in some species (see also, Fiedler, 1951; and Sims, 1955, p. 381). In these birds, the M. p. ventralis would be completely covered by the M. p. dorsalis and invisible when the jaw muscles are viewed through the orbit. Dissection of other passerine birds showed that the M. p. dorsalis lateralis covers much of the M. p. ventralis lateralis and that the M. p. ventralis medialis is usually not visible when the muscles are viewed through the orbit. Only in the thin-billed species can much of the ventral portions of the M. pterygoideus—usually the M. p. ventralis lateralis—be seen when the dorsal aspect of this muscle is examined through the orbit. In any case, the ventral parts of the M. pterygoideus are visible between the two dorsal parts of this muscle, not lateral to both dorsal segments as shown by Beecher. Consequently, his identifications of the parts of the M. pterygoideus would seem to be wrong and should

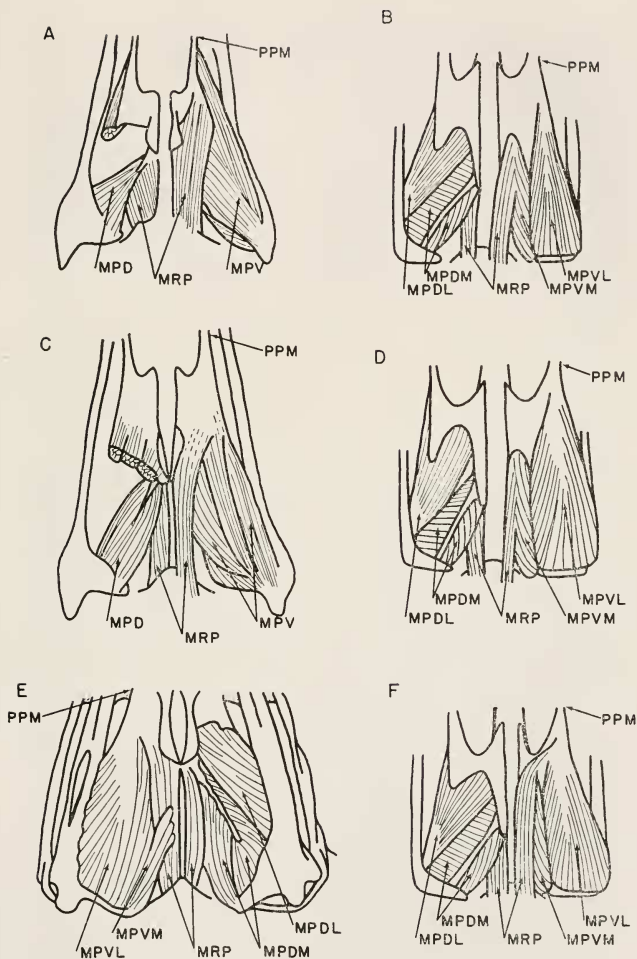


Figure 13. Jaw muscles of: (A) *Toxostoma redivivum* (redrawn from Engels, 1940); (B) *Toxostoma rufum*; (C) *Nesomimus* (redrawn from Engels, 1940); (D) *Dumetella*; (E) *Turdus* (redrawn from Fiedler, 1951); and (F) *Turdus migratorius*.

be corrected. His *M. p. dorsalis anterior* and *M. p. d. posterior* are the two parts of the *M. p. dorsalis medialis* which are anterior and posterior to the pterygoid respectively. His *M. p. ventralis anterior* is the *M. p. dorsalis lateralis*. Thus, his *M. p. ventralis posterior* would be part of the *M. p. ventralis* and most likely the *M. p. ventralis lateralis*. The fifth portion shown in some figures would be the *M. p. ventralis medialis*. However, there is some doubt as to the identification of the ventral parts of the *M. pterygoideus* shown in Beecher's figures. In some cases, his *M. p. ventralis posterior* may be the *M. p. ventralis medialis* instead of the *M. p. v. lateralis*, or, more likely, two muscles should have been shown instead of just one. I may add, at this point, that the only way to be certain of the identification of the parts of the *M. pterygoideus* is to dissect them from the ventral side of the muscle. These misidentifications and the tacit assumption that the *M. pterygoideus* only retracts the palate invalidate Beecher's remarks on the structure and the function of the *M. pterygoideus*.

Here may be the best place to interject a few comments on the factual parts of Beecher's work as there are a number of discrepancies between his drawings and my dissections of the same bird or a species within the same family. For example, Beecher shows the medial slip of the *M. adductor mandibulae* in the larks (1953, p. 316) as a parallel-fibered muscle, but in my dissection of the same species, this muscle was complexly pinnate. Again, Beecher shows the same muscle slip in the Icteridae as pinnate (1953, p. 308), although he showed it as parallel-fibered in his earlier paper (1951a). My dissections of several genera of the Icteridae, including the cowbird, agree with his earlier paper. In both his dissections and drawings, Beecher studied only the external aspect of the muscles and did not dissect the muscles themselves, nor did he attempt to ascertain the mass or cross-sectional area of the muscles. Thus a muscle is considered to be important if it exhibits a large surface area as shown in his drawings. All pinnate muscles are lumped together as one type and automatically considered to be better and more efficient than parallel-fibered muscles. Aside from these points, there are many interpretations which do not seem to agree with the facts presented. For example, the drawings of the adductor (= medial) slip of the *M. adductor mandibulae* do not agree with his separation of the oscine families into two superfamilies on the basis of a pinnate slip in the one group and a parallel-fibered slip in the other group. Nor can I understand the evolu-

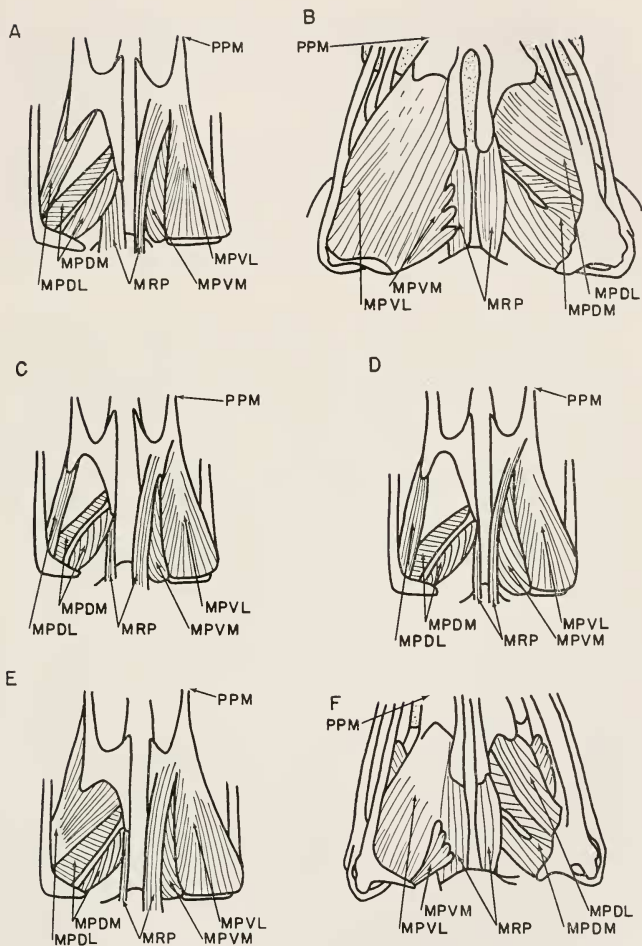


Figure 14. Jaw muscles of: (A) *Hylocichla*; (B) *Paradoxornis* (redrawn from Fiedler, 1951); (C) *Regulus*; (D) *Polioptila*; (E) *Parus*; and (F) *Sitta* (redrawn from Fiedler, 1951).

tionary shift of the muscle fibers from the *M. adductor mandibulae* to the *M. pseudotemporalis superficialis* (Beecher, 1951b, p. 278). However, Beecher's functional discussions are excellent and should be read by those interested in the functional anatomy of the avian skull.

Yet, this critical evaluation of Beecher's work should not be interpreted as meaning that the jaw muscles cannot supply good clues to the relationships and evolution of the passerine birds. They may well prove to be useful if analyzed with extreme caution and with the realization that they are subject to the same evolutionary phenomena, such as convergence, that make the study of any taxonomic character difficult (see also Starek, 1959).

Comparison of the adaptive pathways for increased force of the bite in the passerine birds. I have mentioned above that the major modifications of the palatine process in the passerine birds appear to be associated with the functional demands of seed-eating. However, the relationship between seed-eating and the structure of the palatine process is not a simple one such as the free palatine process (cardinal condition) becoming more and more fused as the *M. pterygoideus* decreases in size (Tordoff, 1954a, p. 12) and vice versa. If this were true, then why do the heavy-billed cardueline finches lack the free palatine process and possess lateral flanges on the anterior end of the prepalatine processes? This question leads to the fundamental question of the entire problem: What are the basic requirements for seed-eating, and how have passerine birds evolved the necessary structural adaptations to meet these demands?

Aside from behavioral traits and such morphological features as the length of the gut (see Eber, 1956), the necessary digestive enzymes and so forth, the basic requirement of a seed-eating bird is to be able to crack the hard shell of a seed without damage to itself. One way to meet this requirement is to grind the seeds in the muscular gizzard, as done by gallinaceous birds and pigeons. Passerine birds have not utilized this method, but crack seeds by means of a powerful closing of their bill. Thus, seed-eating passerines must be able to crack seeds in their bill without damaging the structures of the head, especially the brain and sense organs. Larks are apparently an exception for they swallow seeds whole and grind them in their gizzard (Meinertzhagen, 1951, p. 84). The central problem of this section is, therefore: What are the ways by which a passerine bird might increase the strength of its bite and at the same time protect the

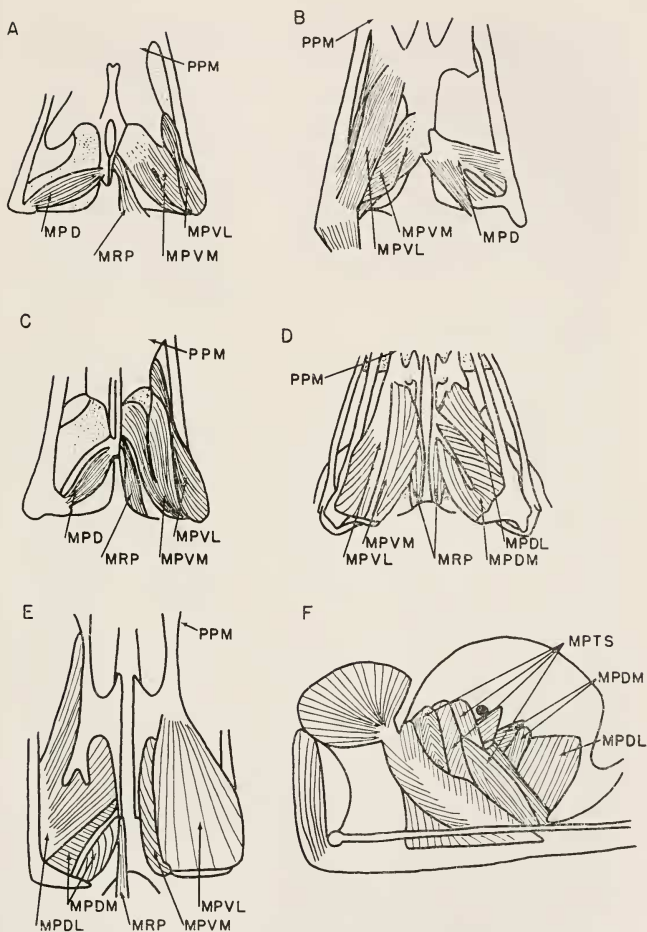


Figure 15. Jaw muscles of: (A) *Cinnyris* (redrawn from Moller, 1930); (B) *Zosterops* (redrawn from Moller, 1931); (C) *Anthornis* (redrawn from Moller, 1931); (D) *Emberiza* (redrawn from Fiedler, 1951); and (E and F) *Passerella*.

other structures of its head against the forces and shocks associated with seed-cracking? The several methods by which the strength of the bite can be increased will be described first, and then it will be shown how different combinations of these methods have evolved in the several groups of finches.

Muscles that close the bill. Four separate jaw muscles in the Passereres act to close the bill, either by raising the mandible or by depressing the upper jaw. Increase in the mass of any of these muscles would increase the strength of the bite. The usual condition in the finches is that all of these muscles have increased in size, but that the relative increase of the several muscles differs in the different groups. The descriptions of the jaw muscles will be for the gray jay (Fig. 11), with comparative notes on their structure in the finches.

a) *M. adductor mandibulae*. This is usually the largest of the jaw muscles or is second in mass only to the *M. pterygoideus*. Without doubt, it is the most complex of the jaw muscles. The *M. adductor mandibulae* is the most posterior of the dorsal adductors of the mandible and takes origin from the lateral side of the skull posterior to the orbit, and from the outer rim of the orbit, and inserts on the dorsal edge and lateral side of the mandible. The action of the *M. adductor mandibulae* is to raise the mandible, but because of the anterior position of its insertion, it is probably most important when the mandible is more than half closed. The anterior position of its insertion gives the *M. adductor mandibulae* a mechanical advantage through increased leverage (the farther a force is applied from the fulcrum point, which in this case is the quadrate-articular hinge, the greater is the resulting force). The anterior insertion also results in a mechanical disadvantage when the bill is wide open because of the unfavorable angle of insertion — a very acute angle which means that most of the strength of the muscle is lost (see Mollier, 1937; and Dullemeijer, 1951, for a discussion of the “unprofitable” angle of insertion). The *M. adductor mandibulae* usually does not leave a muscle scar on the roof of the skull in passerine birds, but in several of the heavy-billed finches, such as the evening grosbeak and the cardinal, a slight depression can be seen on the roof of the skull outlining its area of insertion.

b) *M. pseudotemporalis superficialis*. This tripartite (sometimes bipartite) muscle originates from the posterodorsal wall of the orbit, just medial to the origin of the *M. adductor mandibulae*, and inserts on the medial side of the mandible close to the quadrate hinge. Its action is to raise the mandible, but in

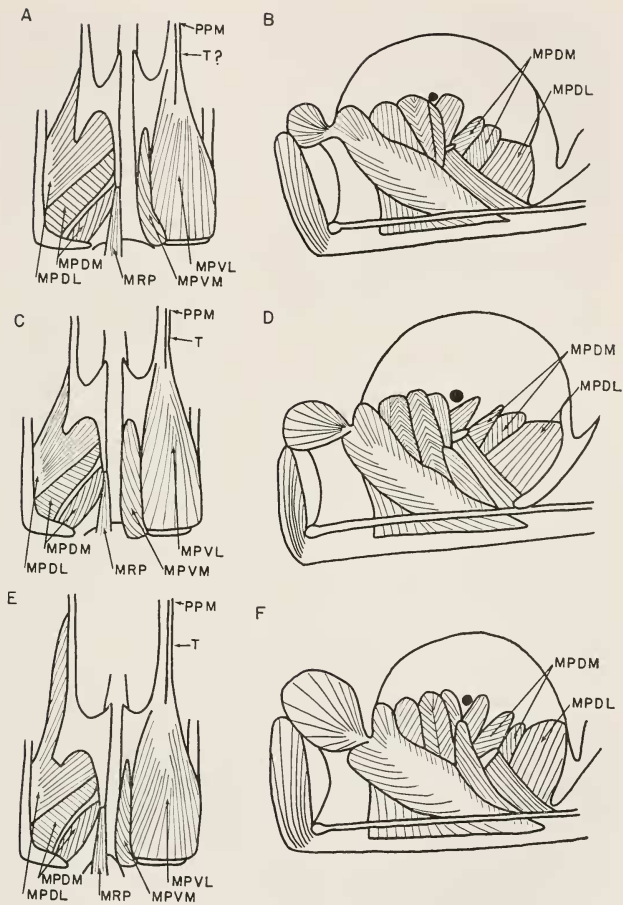


Figure 16. Jaw muscles of: (A and B) *Spizella*; (C and D) *Zonotrichia*; and (E and F) *Pipilo*.

contrast to the *M. adductor mandibulae*, the *M. pseudotemporalis superficialis* is probably more important as an adductor of the mandible when the bill is opened widely. Its insertion close to the quadrate hinge allows it to close the bill rapidly at the price of a reduction of the exerted force. It is interesting that in the cardueline finches, the enlarged part of the *M. pseudotemporalis superficialis* has the most anterior insertion. The large mass and importance of this muscle in the finches is indicated by the several bony processes on the posterodorsal wall of the orbit to which this muscle attaches. These processes are absent in most other passerine birds, especially in the thin-billed insect-eaters.

c) *M. pseudotemporalis profundus*. This muscle originates from the orbital process of the quadrate and inserts on the medial side of the mandible anterior to its insertion of the *M. p. superficialis* and opposite the insertion of the *M. adductor mandibulae*. Like the *M. pterygoideus*, this muscle has the dual function of raising the lower jaw and depressing the upper jaw; however, it is difficult to determine which of these functions is the most important. The *M. pseudotemporalis profundus* is a relatively small muscle as compared to the other jaw muscles, especially the other adductors of the mandible. Increase in the mass of this muscle could serve for increased strength of the adductors of the mandible or for increased strength of the palatine retractors (= depressors of the upper jaw). The latter function may be the more important because this muscle is relatively small in the finches. It is also possible that the *M. p. profundus* functions to oppose the outward forces of the *M. adductor mandibulae* and to strengthen the quadrate hinge.

d) *M. pterygoideus*. This muscle is the most anterior of the jaw muscles and lies ventral and anterior to the *M. pseudotemporalis profundus*. The *M. protractor quadrati* lies dorsal to the *M. pterygoideus* and separates it from the *M. pseudotemporalis superficialis*. The *M. pterygoideus* has already been described and discussed. I need only to emphasize that the medial parts of the *M. pterygoideus* — the depressors of the upper jaw — are relatively more highly developed in groups with a highly kinetic upper jaw while the lateral subdivisions are more highly developed in the groups which have only a slightly kinetic upper jaw. In the finches, only the dorsal portions of the *M. pterygoideus* can be seen through the orbit.

Gross muscle function. The action of a muscle depends not only upon its size and attachment, but upon the orientation of its fibers. In some muscles, the fibers run parallel to one another

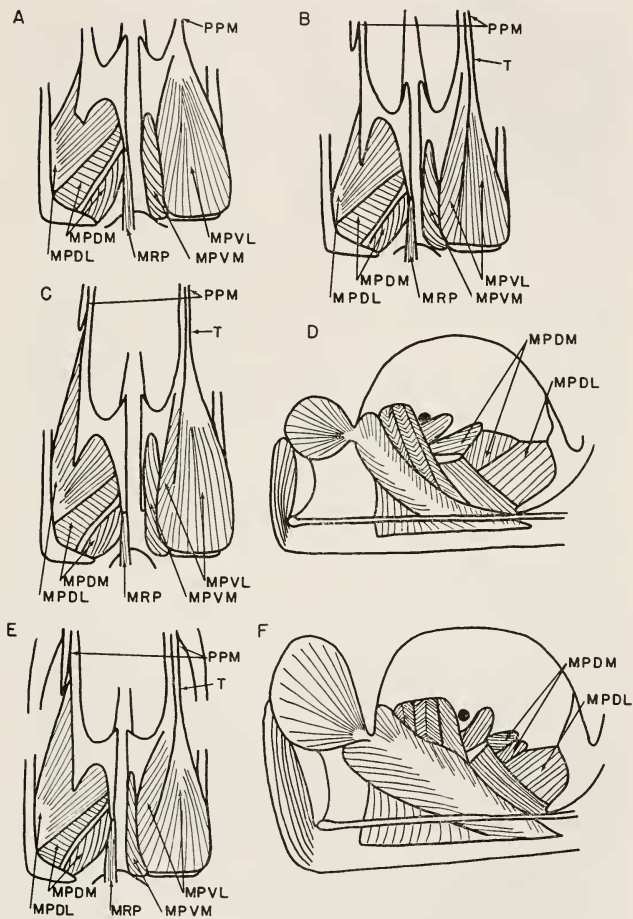


Figure 17. Jaw muscles of: (A) *Melospiza*; (B) *Piranga*; (C and D) *Passerina*; and (E and F) *Cardinalis*.

and to the longitudinal axis of the muscle, while in others, the fibers are oblique to the longitudinal axis and insert on a tendon or an aponeurosis. The former are usually called parallel-fibered or simple muscles, and the latter, pinnate or complex muscles. Pinnate muscles are not identical in their internal structure, but vary greatly in the number of central tendons and in the directions of their fibers. The action of parallel-fibered muscles is relatively easy to analyze. Since all of the muscle fibers are oriented along the longitudinal axis of the muscle, the speed, strength and distance of the muscle contraction is proportional to the number of fibers that have contracted. The angle of insertion of the muscle fibers on the central tendon and the change in this angle during contraction must be considered in addition to these factors when one analyzes the action of a pinnate muscle. Few workers have considered pinnate muscles in detail with the result that virtually nothing is known about their action. Pfuhl (1936) is the only worker, to my knowledge, who has attempted to analyze pinnate muscles with the use of trigonometrical models. The reader is referred to his paper and those by Mollier (1937) and Dullemeijer (1951).

Both parallel-fibered and pinnate muscles are found in the jaw muscles of passerine birds; indeed, some of the jaw muscles, such as the *M. adductor mandibulae*, are among the most complex muscles found in birds. The same muscle may be parallel-fibered in some species and pinnate in others. Some workers, notably Beecher, have differentiated between parallel-fibered and pinnate muscles in their functional discussions. But their basic assumptions are so simplified that their results are misleading. In general, they have assumed that pinnate muscles are one type and parallel-fibered muscles are another, that pinnate muscles are universally more efficient (i.e., stronger) than parallel-fibered muscles and that pinnate muscles have evolved only in response to a selection force for increased strength. In an attempt to clarify some of these problems, I have started an analysis of the action of pinnate muscles using trigonometrical models and hope to present the results in the near future. A few tentative conclusions will, however, be outlined to illustrate the major aspects in the action of pinnate muscles.

The angle of insertion of the muscle fibers on the central tendon determines the relative number of fibers, the relative amount of useful force and the relative speed of central tendon. If pinnate muscles of equal lengths and diameters are compared, the number of fibers increases, the amount of useful force decreases

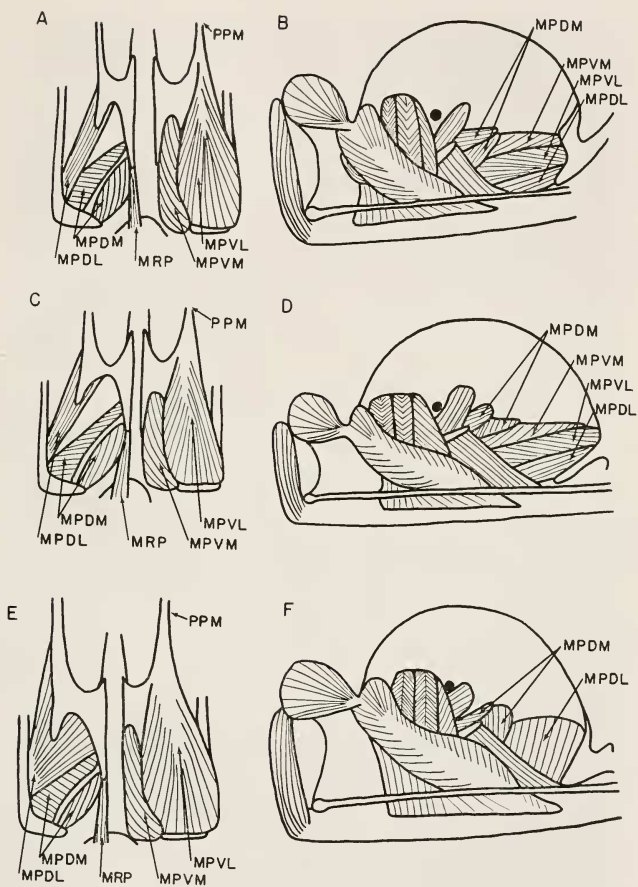


Figure 18. Jaw muscles of: (A and B) *Vireo*; (C and D) *Seiurus*; and (E and F) *Molothrus*.

and the relative speed increases as the angle of insertion of the fibers increases. Similarly, during contraction, the angle of insertion increases with a corresponding decrease in the amount of useful force and an increase in speed. Thus it can be seen that pinnate muscles can be not only strong muscles acting over a short distance, but also weak, rapid muscles acting over a long distance. For example, the *M. pseudotemporalis superficialis* is frequently pinnate. This muscle inserts on the mandible close to the quadrate hinge; hence it serves to raise the mandible rapidly, but with little force. Most likely, it has become pinnate in response to a selection force for increased speed. On the other hand, the *M. adductor mandibulae* is a "power muscle." It inserts on the mandible far anterior of the quadrate hinge and serves to raise the mandible with great force. Also, its action is frequently over a very short distance as, for example, when a finch cracks a seed. Thus, this muscle has become pinnate in response to a selection force for increased strength.

Unless complex pinnate muscles, such as the jaw muscles, are dissected in great detail and all possible reasons for their becoming pinnate are considered, it is better to omit this factor from consideration. For this reason, I have not attempted to compare the pinnateness of the several jaw muscles in the finches. But it is obvious that the degree of pinnateness cannot be omitted if we hope to understand the function of the jaw muscles and to compare properly the jaw muscles of different groups of passerine birds. Thus, in investigations of the jaw muscles, there is really no choice but to dissect the pinnate muscles in great detail and to take great care in interpreting their functional significance.

Relationship between the processes of the skull. Another factor influencing the strength of the bite, but quite apart from the muscles themselves, is the size, shape, and spatial relationships of the various bony processes to which the muscles attach. Changes in these processes would modify the leverage of the jaw muscles. The role of leverage in the action of the jaw muscles has been studied extensively by Kripp (1935) and more recently by Fisher (1955). However, most workers completely overlook the importance of the bony processes in the action of the jaw muscles. A notable exception is Beecher's discussion (1951a, p. 420) of the orbital process of the quadrate. He shows this process to be a lever and discusses the functional significance of the difference in its length in two genera of blackbirds.

The variation in several bony processes of the skull is directly correlated with changes in the jaw muscles. Some examples are

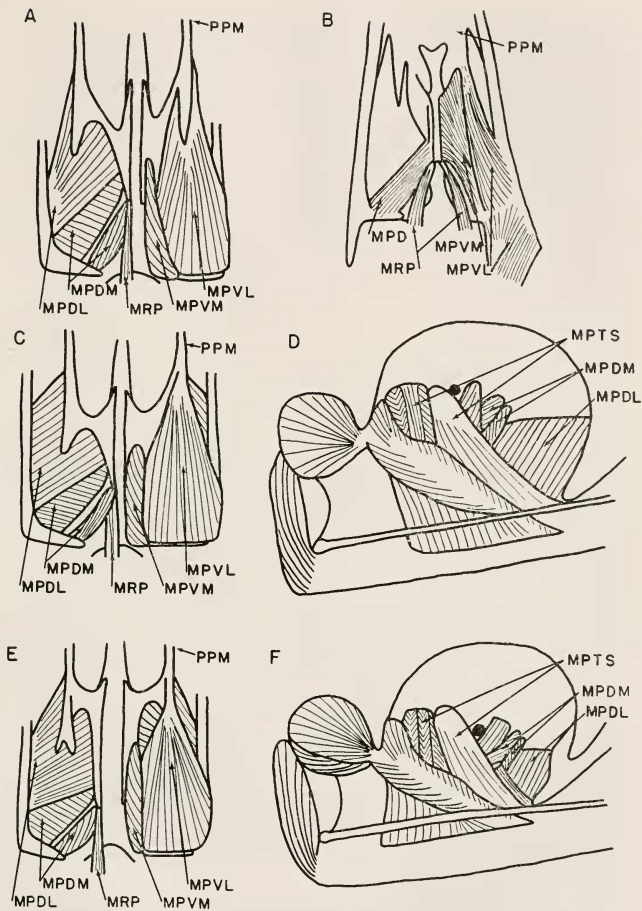


Figure 19. Jaw muscles of: (A) *Quiscatus*; (B) *Dacnis* (redrawn from Moller, 1931); (C and D) *Fringilla*; and (E and F) *Spinus*.

the size of the medial process of the mandible, the length of the transpalatine process (and hence the distance between this bone and the mandible), the length of the palatines themselves, the size of the auditory bullae ("inflated squamosal region" Tordoff, 1954a, pp. 9-10, which is associated with the mass and length of the *M. depressor mandibulae*), and finally, the free palatine process of the premaxilla as seen in the cardinals. This list could be easily expanded, but it is sufficient to show that a comparative study of the musculature of so complex a system as the jaw muscles must include the detailed mechanics of the underlying bone-lever system. The converse is also true; a study of the skull must also include the muscles and other influencing factors.

Comparison of the jaw muscles in the finches. The jaw muscles of the "nine-primaried" and "ploceid" finches will now be compared, using the information presented in the preceding sections. The major question to be answered is: Has the same morphological adaptation for cracking seeds evolved in the several groups of finches, or have different adaptations evolved in these groups (cf. multiple pathways of evolution)? This question may appear to be unrelated to the central problem of this paper — the evolution of the palatine process of the premaxilla — especially when the jaw musculature of the finches is compared, but it is essential to study the entire set of jaw muscles before the differences in the *M. pterygoideus* can be understood and its correlation with the palatine process of the premaxilla clarified. In addition to comparing the jaw muscles of the several groups of finches, I shall compare, whenever possible, a small-billed species with a large-billed species of the same group, to determine whether there is any variation in the jaw muscles within families or subfamilies of passerine birds and more precisely, whether the jaw muscles have changed within a group of finches to meet the demands of a stronger bite. I shall describe the small-billed species first and then compare it to the large-billed species. This procedure is used for convenience only and not to imply that the small-billed species is primitive in the group or that evolution in the finches has always been from the small- to the large-billed size.

The jaw muscles of a warbler (*Sciurus aurocapillus*, Figs. 18C and 18D) and a vireo (*Vireo olivaceus*, Figs. 18A and 18B) — both insect-eaters with thin bills — and included, in addition to those of the gray jay, for comparison with the heavy-billed seed-eaters. These species were chosen because of convenience only and not because of any special relationship to the finch groups

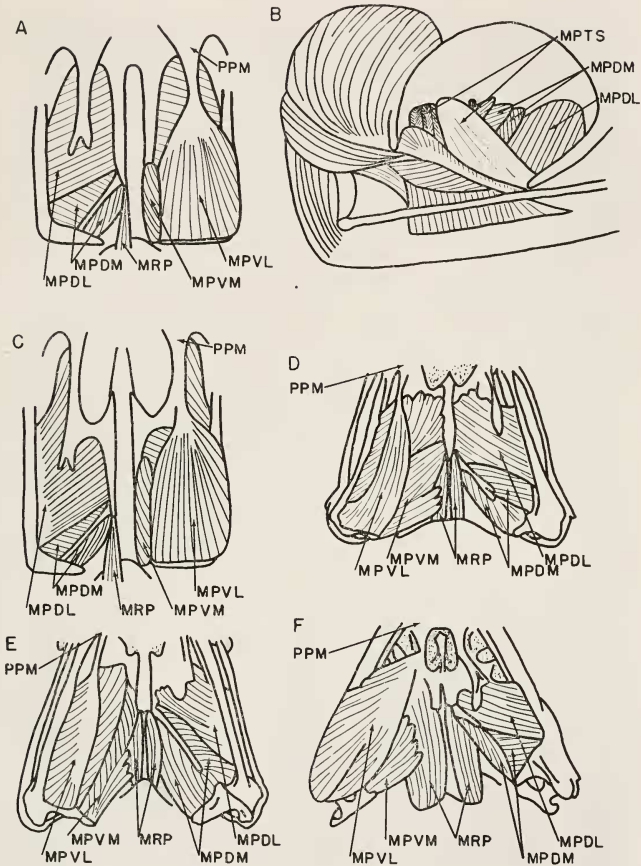


Figure 20. Jaw muscles of: (A and B) *Hesperiphona*; (C) *Carpodacus*; (D) *Carduelis* (redrawn from Fiedler, 1951); (E) *Pinicola* (redrawn from Fiedler, 1951); and (F) *Loxia* (redrawn from Fiedler, 1951).

discussed here. When examining the jaw muscles of these insectivorous birds, the general impression one receives is that the muscles are weakly developed, or, to put it in another way, the muscles are not overly developed and do not show any specializations for a strong bite. For example, the origin of the *M. adductor mandibulae* has not spread over the roof of the skull and the *M. pseudotemporalis superficialis* has not expanded to cover the *M. p. profundus*. One of the most striking features in the jaw muscles of these species is the relative weakness of the parts of the *M. pterygoideus* that adduct the mandible, especially the *M. p. dorsalis lateralis*. In the warbler and the vireo, parts of the *M. p. ventralis* may be seen between the two halves of the *M. p. dorsalis* when the jaw muscles are viewed through the orbit—an indication of the weakness of the *M. p. dorsalis lateralis*. This muscle is large in the gray jay.

The emberizine finches. The emberizine finches may be considered as generalized or, better, as unspecialized seed-eating birds; they feed on smaller seeds and are more insectivorous than most other groups of finches. In accordance with these feeding habits, the morphological specializations for seed-eating are less developed than in other finches. For example, the bill of the emberizines, although shorter and stouter than the bill of insectivorous birds, is longer and thinner than the bill of other groups of finches. The palatine process of the premaxilla is essentially the same as in the insect-eaters; it lies along the prepalatine process and is more or less fused with that bone. The major exceptions are *Melopyrrha* and *Tiaris*, which have a free palatine process such as is found in the cardinals, and *Oryzoborus*, which has a lateral flange on the prepalatine process similar to that found in the cardueline finches. These "aberrant" genera will be discussed in the section on relationships. The emberizine finches are a useful starting point, for their lack of extreme specializations in the skull and in the jaw muscles allows us to analyze the basic modifications in these structures for seed-cracking. Insectivorous and granivorous birds are not sharply distinct types, but grade into one another; hence, it is not always possible to distinguish insectivorous from granivorous adaptations.

The jaw muscles of a field sparrow (*Spizella pusilla*, Figs. 16A and 16B) are similar to those of the warbler and the vireo except for the increase in mass of the mandible adductors. The *M. adductor mandibulae* and the *M. pseudotemporalis superficialis* are larger and more pinnate than those in the warbler, but they

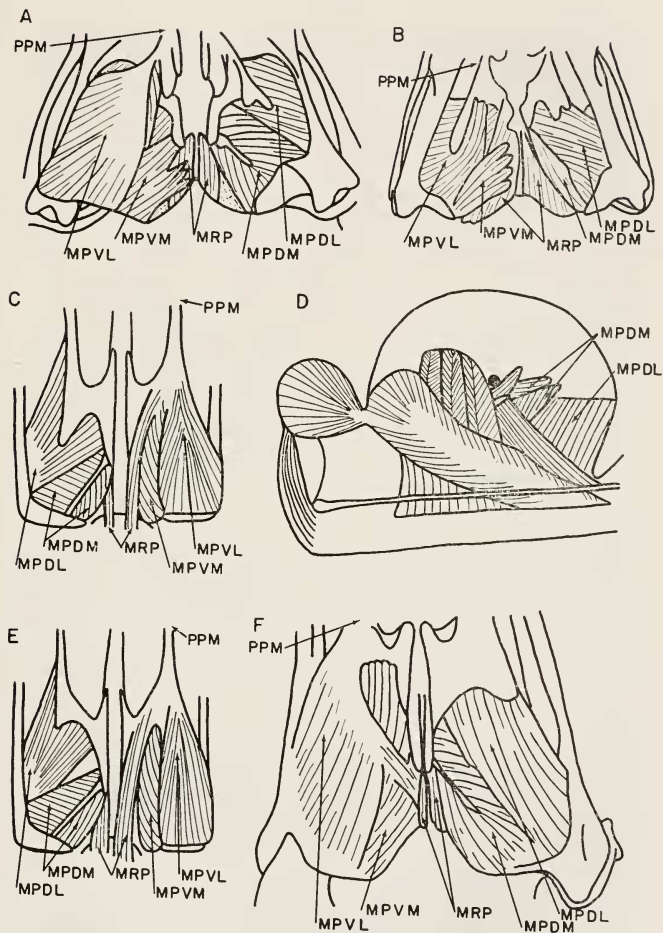


Figure 21. Jaw muscles of: (A) *Coccothraustes* (redrawn from Fiedler, 1951); (B) *Lonchura* (redrawn from Fiedler, 1951); (C and D) *Passer*; (E) *Sturnus*; and (F) *Corvus* (redrawn from Fiedler, 1951).

are quite similar in other respects. The *M. pseudotemporalis profundus* is not hidden by the *M. p. superficialis* as in the cardueline finches. Most striking is the expansion of the *M. pterygoideus dorsalis lateralis* which completely covers the ventral parts of the *M. pterygoideus*. Turning to the ventral aspect of the *M. pterygoideus*, the increase of the mandible adductors at the expense of the palate retractors can be readily seen. Yet the palate retractors are still relatively large. A tendon of the *M. pterygoideus ventralis lateralis* appears to extend forward along the palatine to the position of the semifused palatine process of the premaxilla. I have shown this tendon running forward in my drawing of the field sparrow (Fig. 16B), but wish to emphasize that it is not certain whether this tendon really exists. The small size of the field sparrow makes it difficult to determine whether the strip of connective tissue seen along the prepalatine process is the periosteum of that bone or a tendon of the *M. pterygoideus*. This problem may be resolved by histological examination, but I am not sure whether it can ever be decided beyond all doubt. Therefore, although there is an indication in the field sparrow of a direct association between the *M. pterygoideus* and the palatine process by means of a tendon, this must still be proven.

In such a medium-billed species as the white-throated sparrow (*Zonotrichia albicollis*, Figs. 16C and 16D) and the larger rufous-sided towhee (*Pipilo erythrophthalmus*, Figs. 16E and 16F), the jaw muscles increase in mass as the size of the bill increases. In the towhee, there is a muscle scar on the roof of the skull outlining the origin of the *M. adductor mandibulae*, a reflection of the increase in size of this muscle. The most conspicuous changes in the muscles are, however, the increase in size of the antero-medial part of the *M. pseudotemporalis superficialis* toward the cardueline condition and the increase in the adductor parts of the *M. pterygoideus*. Both the *M. p. dorsalis lateralis* and the *M. p. ventralis lateralis* increased in mass. The change in the *M. p. v. lateralis* is of particular interest. The lateralmost fibers of this muscle converge on a tendon that runs along the lateral edge of the palatine up to the fused palatine process of the premaxilla. Although this tendon is easily destroyed during dissection, it can readily be demonstrated in the towhee. The tendon is intimately associated with the periosteum of the palatine. In the smaller species, even if it is present, the tendon is almost indistinguishable from the periosteum of the palatine, as for example in the field sparrow. The towhee, the largest of these

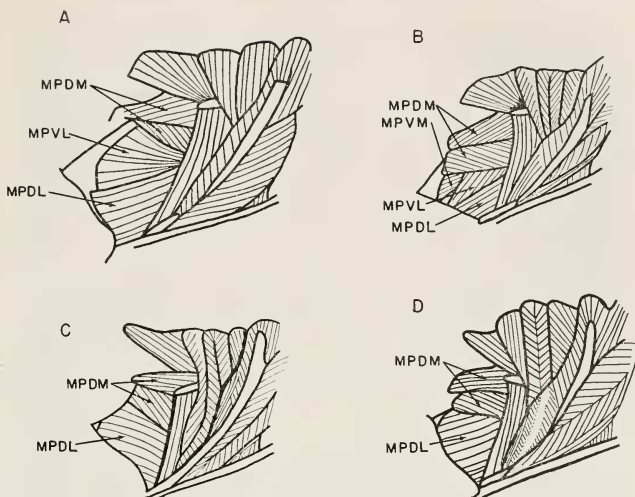


Figure 22. Jaw muscles as seen through the orbit of: (A) *Phylloscopus*; (B) *Oporornis*; (C) *Melospiza*; and (D) *Molothrus* (redrawn from Beecher, 1953). The *M. pterygoideus* has been labeled according to my identification. Beecher's identifications for *Phylloscopus* are: *M. pterygoideus dorsalis anterior* (3a) = MPDM (anterior half); *M. p. dorsalis posterior* (3b) = MPDM (posterior half); *M. p. ventralis anterior* (4a) = MPDL; *M. p. ventralis posterior* (4b) = MPVL (usually, but sometimes part or all of the MPVM is included in this muscle by Beecher).

species, has a well-developed tendon very similar to the tendon of the *M. p. ventralis lateralis* that attaches to the free palatine process of the premaxilla in the tanagers and the cardinals. Thus, with increase in the size of the bill in these species of emberizine finches, the *M. pseudotemporalis superficialis* changes toward the cardueline condition while the *M. pterygoideus* changes toward the cardinal condition.

Not all emberizine finches show these changes in the structure of the jaw muscles. The fox sparrow (*Passerella iliaca*, Figs. 15E and 15F), another heavy-billed species, tends toward the cardueline condition not only in the structure of its *M. pseudotemporalis superficialis*, but also in the structure of its *M. pterygoideus ventralis lateralis*. The lateralmost fibers of this latter muscle do not send a long tendon forward along the palatine, but rather insert on the distal tip of the transpalatine process by means of

a short tendon. In accordance with this condition of the *M. p. v. lateralis*, the tip of the transpalatine process is forked in a manner similar to that seen in the cardueline finches. The lateral branch of the transpalatine process is associated with the fibers inserting on the medial side of the mandible while the medial branch is associated with the fibers inserting on the medial process of the mandible. Thus, the changes in the structure of the jaw muscles in the fox sparrow are exclusively toward the cardueline condition. I have dissected a specimen of the Lincoln sparrow (*Melospiza lincolnii*) and a specimen of the song sparrow (*Melospiza melodea*, Fig. 17A). These species are smaller than the fox sparrow and consequently have smaller (both absolute and relative) jaw muscles. Nevertheless, the structure of their *M. pseudotemporalis* and their *M. pterygoideus ventralis lateralis* is similar to those seen in the fox sparrow. It is, however, not certain whether these species lack the lateral tendon as seen in the fox sparrow, or have the tendon which was overlooked because of the small size of these species.

In the emberizine finches, all of the adductor muscles of the mandible and the retractors of the palate have increased in size. This increase is relatively "even" in that one adductor or retractor has not assumed a highly dominant role in closing the bill. Sims (1955, p. 382) points out that the "division of labor" between the several muscles which close the bill has two important attributes. First, it spreads the origin of these muscles and hence the strain on the bones over a larger area of the skull. Second, the "harmful" components of force are counteracted. For example, the *M. adductor mandibulae* tends to pull the mandible backwards and outwards as well as upwards. These backward and outward forces are counteracted by the *M. pterygoideus* which pulls the mandible inward and forward as well as upward and by the *M. pseudotemporalis superficialis* and the *M. p. profundus*, both of which have inward and backward components as well as upward components of force. If only one of these adductors were powerfully developed, as for example, the *M. adductor mandibulae*, it might put uneven forces on the mandible and possibly might even disarticulate it during a particularly powerful contraction. This would, however, never happen because the jaw muscles function and evolve as a unit. Consider, for example, a bird which is becoming a seed-eater and thus subject to a selection force for a larger bill and stronger jaw muscles. As soon as one adductor begins to become disproportionately large, it would put an uneven strain on the mandible.

The other adductors must enlarge to counteract its "harmful" components of force or the bird will have a selective disadvantage. If the other adductors did not enlarge, the bird would be selected against long before the one muscle became large enough to disarticulate the mandible.

Compared to a warbler or a vireo skull, the skull of an emberizine finch is a more substantial structure with a shorter and heavier bill and a stouter palate. Yet, it cannot be called a reinforced skull, for the interorbital septum and the anterior part of the interpalatine space are both unossified. Nevertheless, there are other skeletal adaptations for seed-eating, such as the bony processes on the posterior wall of the orbit and on the lateral side of the skull, which are directly correlated with the increase in the mass of the adductor muscles, but these do not need to be considered separately. One of the most important features of the skull is the fact that the upper jaw has retained its kinetic property, which plays a large role in the seed-cracking method of the emberizines.

In the emberizines, a seed to be cracked is held between the jaws just anterior to the angle of the mandible. This is approximately the point where the palatine meets the premaxilla, where the nasal process of the maxilla meets the body of the maxilla, and where the horny covering of the upper jaw ends. This point is just anterior to the insertions of the adductor muscles — hence as close as possible to the jaw articulation and the point where the maximum force may be exerted on the seed — and yet it is still the most reinforced part of the skull. When the adductor and retractor muscles contract, the upper jaw is depressed and the lower jaw is raised until the seed coat is cracked. This pincer action can be compared to the cracking of the shell of a nut by means of a nutcracker or a pair of pliers. The chief advantage of the "nutcracker" method is that the initial shocks are borne by the jaws which form a system partially isolated from the braincase. This system permits the retention of a lighter skull and eliminates the need for reinforcement of the braincase. A light skull has a lower inertia which means that smaller muscles are needed to move it — a distinct advantage for a flying animal. Such a light skull and a faster-closing bill enables the emberizine finches to capture insects, but also limits them to smaller seeds.

The cardinaline finches. The cardinaline finches feed, as a rule, more exclusively on seeds and perhaps on larger seeds than do the emberizine finches; therefore, it is not surprising that they

possess more specialized modifications for seed-eating. They have a shorter and more conical bill with a more decurved upper jaw and a greater angle in their mandible than the emberizines. The most conspicuous specialization, however, is the palatine process of the premaxilla, which lies free of the palatine and is situated in the space between the palate and the jugal bar. The other osteological features of the cardinaline skull will be described below.

The jaw muscles of the indigo bunting (*Passerina cyanea*, Figs. 17C and 17D), when viewed through the orbit, are very similar to those of the field sparrow. The M. adductor mandibulae has expanded over a larger area of the roof of the skull, but otherwise the differences between these species appear to be minor ones of proportions. However, the M. pterygoideus of the indigo bunting, when viewed from beneath, is unlike that seen in the field sparrow. The superficial fibers on the lateral half of the M. p. ventralis lateralis form a distinct bundle that originates from the free palatine process of the premaxilla by means of a separate tendon. These fibers and tendon would correspond to the lateral fibers and tendon seen in the towhee. Examination of the rest of the M. pterygoideus shows that the palatine retractors are still well developed.

The cardinal (*Cardinalis cardinalis*, Figs. 17E and 17F) is one of the largest-billed members of this group. Most of its jaw muscles, as seen through the orbit, are similar to those of the indigo bunting except for the M. adductor mandibulae, which has become larger and has spread over the roof of the skull. In fact, this muscle leaves a clearly visible muscle scar outlining its area of origin on the roof of the skull. The M. pterygoideus, especially its lateral subdivisions, has also enlarged greatly. Again, the lateral and superficial part of the M. p. ventralis lateralis originates by means of a tendon from the palatine process of the premaxilla. These fibers comprise less than 5 per cent of the total mass of the M. pterygoideus, not 25 per cent as Tordoff estimates. The functional significance of this separate bundle of fibers will be discussed later. It is interesting to note that there has been no expansion of the medial part of the M. pseudotemporalis superficialis in the cardinals. Possibly, the genetic capacity for this structure had never appeared in the cardinals or perhaps this muscle cannot function in harmony with the superficial bundle of the M. p. ventralis lateralis.

The fact that the cardinals feed more exclusively on seeds is reflected in the structure of their skull as well as in the jaw

muscles. The bill is shorter and broader, and the bones of the palate are stouter than those in the emberizine finches. The entire skull is reinforced; the nasal septum and the anterior interpalatine space are ossified, the maxillo-palatines are fused to the vomer and the nasal process of the maxilla is at right angles to the body of the mandible and parallel to the force on the upper jaw. Yet, the upper jaw has retained its kinetic property—a fact that is reflected in the fusion between the vomer and the maxillo-palatines and in the medial ossification at the jugal-maxilla connection, both of which are absent in the cardueline finches.

The cardinals crack seeds by the nutcracker method as has just been described for the emberizines; the mobility of the upper jaw permits the use of this method. Thus the cardinals do not need heavy bosses on the upper jaw to protect the braincase. The function of the separate bundle of fibers of the *M. p. ventralis lateralis* is still a problem. Obviously it serves some particular function, for its structure is relatively constant within the cardinals—an indication that a selection force responsible for its maintenance is present. These fibers do not appear to play a vital part in cracking seeds; the other adductors of the mandible and retractors of the palate are many times more massive than this bundle of fibers and are probably able to crack seeds without any aid from these superficial fibers of the *M. p. ventralis lateralis*. Because of their greater length and their insertion on the mandible near its articulation and on the ventral rim of the medial process of the mandible, these fibers appear to have as their chief action, the raising of the mandible. These fibers would raise the mandible rapidly because of their insertion on the medial process as has been discussed above (p. 392). I suggest, therefore, that the function of the superficial fibers of the *M. p. ventralis lateralis* is to raise the mandible quickly until the seed or insect is grasped firmly between the jaws. The more massive adductors and retractors would then take over the task of cracking the seed. If this assumption is correct, the origin of the separate bundle of fibers and the free palatine process is a mystery. It does not appear to be an essential modification for seed-eating; indeed, it is somewhat contrary to what would be expected. Perhaps it is a specialization for a fast-closing bill to allow the cardinals to feed on insects as well as on seeds, or perhaps it is a modification of a similar specialization in the insectivorous ancestors of the cardinals (possibly the tanagers?).

The cardueline finches. The carduelines differ from the emberizines and agree with the cardinalines in feeding more on seeds (in fact, the carduelines feed almost exclusively on seeds), and in having a shorter, conical bill with a decurved upper jaw and a greater angle in the mandible. The chaffinch and brambling (*Fringilla*) are exceptions and resemble the emberizines in the structure of their skulls. The similarity between the cardinals and the carduelines is a superficial one, for these groups are strikingly different in the structure of the skull and in the arrangement of the jaw muscles. For example, in the cardueline finches, the palatine process of the premaxilla is completely fused with the palatine, and in its stead is a lateral flange as described above. Again *Fringilla* differs from the rest of the cardueline finches in having an unfused palatine process in the adult and in lacking completely the lateral flange.

The jaw muscles of the goldfinch (*Spinus tristis*, Figs. 19E and 19F), as seen through the orbit, are quite different from those in the emberizine finches or the cardinals. The M. adductor mandibulae is relatively large for a bird the size of a goldfinch, with the portion spread over the roof of the skull doubled—a condition not seen in any other passerine family examined in this study. The M. pseudotemporalis superficialis has enlarged unevenly. Only the anteromedial part of this muscle has enlarged to a great degree; the lateral parts of the M. p. superficialis appear as a small isolated muscle sandwiched between the larger medial portion and the M. adductor mandibulae. The large medial portion of the M. p. superficialis almost completely covers the M. p. profundus. Those muscles associated with the raising and lowering of the upper jaw, the M. p. profundus and the M. protractor quadrati, are relatively small muscles with fleshy origins and insertions. Turning to the ventral side of the head, the large M. pterygoideus can be seen. Again, the mandible adductor parts of this muscle have enlarged while the palatine retractors have decreased in size. Special note should be taken of the M. p. ventralis lateralis. It takes origin only from the transpalatine process; no muscle fibers or tendons run forward to attach to the palatine in the region of the lateral flange. As in the fox sparrow, the tip of the transpalatine process is forked; the lateral branch is associated with the fibers running to the ramus of the mandible while the medial fork is associated with those fibers running backwards to the medial process of the mandible.

If the jaw muscles of a medium-billed species, such as the purple finch (*Carpodacus purpureus*, Fig. 20C), and those of a large-billed species such as the evening grosbeak (*Hesperiphona vespertina*, Figs. 20A and 20B), are examined, two important changes from the goldfinch condition are discernible. First, the M. adductor mandibulae has increased in size until, in the evening grosbeak, its origin spreads over most of the roof of the skull and leaves a well defined muscle scar. Second, the medial part of the M. pseudotemporalis superficialis has increased in mass to dominate the muscles inside the orbit. It completely obscures the M. p. profundus and almost completely hides the M. protractor quadrati and the lateral part of the M. pseudotemporalis superficialis. The two major dorsal adductors of the mandible—the M. adductor mandibulae and the medial part of the M. pseudotemporalis superficialis—converge upon the mandible from the outside and the inside respectively—an excellent example of two muscles so placed that their “harmful” effects are counteracted. There are no significant changes other than increase in mass in the structure of the M. pterygoideus.

Sims (1955) has reported on the jaw muscles of the hawfinch (*Coccothraustes coccothraustes*), a species very similar and apparently closely related to the evening grosbeak. Unfortunately, his excellent analysis of the skull and the jaw muscles is marred by several misidentifications, such as the M. quadrato-mandibularis in his figure 4B (this is actually the enlarged medial part of the M. pseudotemporalis superficialis) and the M. p. ventralis lateralis anterioris in his figure 5B (this is probably the M. p. dorsalis lateralis).

I was fortunate in being able to examine two specimens of the chaffinch (*Fringilla coelebs*, Figs. 19C and 19D). In most respects, the jaw muscles are similar to those of the least specialized cardueline finches, although they are not as powerful. The most significant feature of the dorsal adductors is the enlarged medial portion of the M. pseudotemporalis superficialis. This muscle is identical to that in the heavier-billed cardueline finches and, in fact, it completely covers the M. p. profundus, as in the evening grosbeak. The M. adductor mandibulae is larger than expected; its origin has expanded over as large an area of the roof of the skull as in the larger towhee. However, the M. adductor mandibulae of the chaffinch is not as specialized as in the carduelines, but is similar to that seen in the emberizine finches (see Fiedler, 1951, pp. 241-242). Turning to the ventral aspect of the M. pterygoideus, we find that it is almost identical

to that seen in the goldfinch, the main difference being that the chaffinch has a less massive muscle. The unfused palatine process of the premaxilla was clearly visible, but there was no connection between it and the M. p. ventralis lateralis; in fact, the M. pterygoideus of the chaffinch is very reminiscent of that seen in the fox sparrow.

The cardueline finches (with the exception of *Fringilla*, Eber, 1956) feed almost exclusively on seeds and hence have a massive reinforced skull, one that is even heavier than the cardinaline skull. The interorbital septum, the nasal septum, and the interpalatine space are more heavily ossified in the carduelines than in the cardinals. The most conspicuous difference between the two groups is the lack of a free palatine process and the development of a lateral flange on the prepalatine process with an overlying horny pad of rhamphotheca in the cardueline finches. The upper jaw has lost most of its mobility, but the fact that it is not rigidly fused to the cranium as stated by Sims (1955, p. 373) could be ascertained by boiling skulls of *Hesperiphona* and *Coccothraustes* for a minute or two as suggested by Beecher (1951a, p. 412). This technique softens the dried ligaments and restores flexibility to the skull. However, Sims' conclusion is still correct, for the upper jaw is essentially stationary during the closing of the bill. The immobile upper jaw plus the presence of the heavy bosses of bone and rhamphotheca suggest that the cardueline finches employ a method other than that of a nutcracker to crack the seed shell.

A seed to be cracked by a cardueline finch is placed in the corner of the mouth, just anterior to the angle of the mandible. The seed lies between the heavy pads of the upper jaw and those of the lower jaw and is held in place by the tongue, as shown by Eber (1956). Upon contraction of the adductor muscles, the mandible is raised and forced against the seed until its shell cracks. In this way, the apparatus resembles the action of a vise. Since the upper jaw is continuous with the braincase, the cracking shock must be transmitted across the skull without harm to it or to the contained organs. The heavy bosses on the upper jaw provide an even distribution of the shock, protecting the braincase and the brain from injury. Perhaps the slight amount of mobility of the upper jaw may partly absorb the shock wave that accompanies the actual cracking of the seed. The heavy pads of rhamphotheca may serve to absorb some of the shock wave, but this is open to question. The vise method is intrinsically

no more efficient than the nutcracker method, but a heavier seed can be cracked with the vise method since the bony elements involved are inherently larger. Not only the palatine complex, but the entire skull is used to transmit the forces and shocks of seed-cracking; hence larger forces are possible for an equal amount of stress on the bone. Sims has shown that the hawfinch must exert a force of 100 to 150 pounds when it cracks an olive stone. However, the powerful vise system is developed at the expense of the mobility of the upper jaw which limits the cardueline finches to a rather exclusive diet of seeds (Eber, 1956). The "slender-billed" chaffinch does not have such a specialized bill and feeds extensively on insects during the summer. It probably uses the "nutcracker" method of cracking seeds rather than the "vise" method.

The above descriptions of the nutcracker and the vise methods of seed-cracking, being based completely upon deductive reasoning from the structure of the skull and the jaw muscles in several groups of finches, have raised more problems than they have solved. First, direct observations or experiments are needed to verify my conclusions as to function and to establish the exact morphological and functional differences between the two methods. It must be emphasized that the important functional difference between the nutcracker and the vise methods of cracking seeds is not in terms of applying force on the seed, but in terms of protecting the braincase from the shocks associated with the breaking of the seed coat. In the nutcracker method, these shocks are isolated within the jaw apparatus, while in the vise method, these shocks are distributed evenly to the braincase by the heavy bosses of bone and rhamphotheca and thus are prevented from concentrating on one bony element. The method used in each group of finches and the degree of specialization in each group must be determined. The difference between the extreme types, such as the cardinals and the carduelines, is clear, but that between the less specialized forms is quite fuzzy. For example, the emberizine finches are best classified as having a "primitive" nutcracker method of seed-cracking. Where is the boundary between the primitive nutcracker method and the specialized nutcracker or the vise methods, both of which are presumed to have evolved from the emberizine condition? I have assumed for the purposes of this paper that the presence of a lateral flange indicates that the vise method is used. Therefore, the estrildids, the advanced ploceids, *Oryzoborus* of the

Emberizinae and *Psittirostra* of the drepaniids would use the vise method of seed-cracking; however, there is no available evidence supporting a correlation between the lateral flange and the vise method. These problems must be solved before we can obtain a complete picture of the evolution of seed-eating in the passerines and of the origin of the several finch-like groups.

Other finches. The jaw muscles of three other seed-eating passerines, the horned lark (*Eremophila alpestris*, Figs. 12C and 12D), the cowbird (*Molothrus ater*, Figs. 18E and 18F), and the house sparrow (*Passer domesticus*, Figs. 21C and 21D) were dissected. Although seeds comprise a large part of the diet of these species, their jaw muscles are relatively unspecialized when compared to those of the cardinaline and the cardueline finches. The jaw muscles of the house sparrow and the cowbird are similar to one another and to those found in the smaller emberizine finches and show the usual development of the adductor muscles. Neither species has any specialization of the *M. pseudotemporalis superficialis* or the *M. pterygoideus*; both have an expansion of the *M. adductor mandibulae* over the side of the skull to about the same extent as in the towhee. The medial part of the *M. adductor mandibulae* is expanded in both species and bulges inward to cover part of the *M. pseudotemporalis profundus*. This slip of the *M. adductor mandibulae* has not become specialized in either species. The upper jaws of the house sparrow and of the cowbird are kinetic, suggesting that these birds probably use the nutcracker method of seed-cracking. In almost all respects, both species are comparable to the emberizine finches in the specialization of their seed-cracking modifications.

The jaw muscles of the horned lark are the most interesting because they have evolved a quite unique specialization (for seed-cracking ?) not found in any other species of passerine birds I have examined. The *M. adductor mandibulae* has not spread over the side of the skull roof as in other seed-eating birds. Instead, the medial part of this muscle has enlarged and become pinnate. This large medial slip of the *M. adductor mandibulae* may be able to provide much of the force needed for cracking seeds that is usually supplied by the lateral parts of this muscle and by the *M. pterygoideus*, both of which are poorly developed in this species. It is also conceivable that this pinnate slip has a special function that is totally independent of seed-cracking. Larks (all species ?) swallow seeds whole and thus would not need strong jaw muscles. More work correlating the feeding

methods with the jaw muscles of the larks is needed before this problem is solved.

Résumé on the feeding methods in the finches. A brief review of the methods of seed-cracking in the three groups of "nine-primaried finches" and the associated adaptations may now be given. The emberizine sparrows (plus the house sparrow and the cowbird) can be regarded as "generalized" seed-eaters, lacking the extreme specializations for seed-cracking. The adductors of the mandible and the retractors of the palate are equally well developed, and the upper jaw has not lost its kinetic property — the result is the nutcracker method of seed-cracking. Some of the larger-billed emberizines (e.g., the towhee) tend toward the cardinals in their jaw muscles, especially in the structure of the *M. pterygoideus*; others (e.g., the fox sparrow) tend toward the cardueline finches. The cardinals are heavy-billed forms that have retained the nutcracker method; hence the skull is still relatively light. Increase in the mass of the *M. pterygoideus ventralis lateralis* and its lateral tendon has resulted in the free palatine process of the premaxilla. The free palatine process and the movable upper jaw probably preclude the development of the lateral flanges on the prepalatines as seen in the cardueline finches. The second group of heavy-billed finches — the carduelines — employ another method of cracking seeds, the vise method. However, a presumed "primitive" genus, *Fringilla*, is quite similar to the fox sparrow in the structure of its jaw muscles and probably uses the nutcracker method. In the specialized carduelines, the upper jaw has lost its mobility; it is a nearly stationary block against which the mandible presses. Heavy bosses of bone (the lateral flanges) and rhamphotheca distribute the shocks associated with the cracking of the seed evenly to all parts of the braincase. Only the adductor muscles are well developed in the cardueline finches; in fact, the muscles associated only with the movement of the upper jaw have become small and are on the verge of becoming functionless.

Conclusions. The primary function of the palatine process of the premaxilla is to provide a point of anchorage for the palatines and hence promote a stronger connection between the palate and the upper jaw. Secondary functions have been superimposed on this primary function in several groups of passerine birds, but these secondary functions do not conflict with the operation of the primary function. The secondary functions have been responsible for the modifications of the palatine process — the development of the free process and the lateral flanges — within

the passerines. Using the data assembled in the preceding pages, I wish to return to the three problems associated with the modifications of the palatine process which have been listed in the beginning of the section on "modifications."

a) Development of the free palatine process: In most groups of passerine birds, there is no connection, either morphologically or functionally, between the *M. pterygoideus* and the palatine process of the premaxilla. Only in a few groups, such as the cardinals and the tanagers, does part of the *M. p. ventralis lateralis* take origin from the palatine process. These groups have a free palatine process. Therefore, it may be concluded that the free palatine process as seen in the cardinals serves as the point of origin for the lateral superficial bundle of the *M. p. ventralis lateralis*. This modification is probably not a specialization for seed-eating as commonly believed, but for rapid rising of the mandible during the early phases of closing the bill, which appears to be a specialization for catching insects.

b) Development of the lateral flange: In a few groups, lateral flanges have developed at the site of the fused palatine processes. These birds have acquired a powerful set of jaw muscles for seed-cracking, but have lost the mobility of the upper jaw. They employ the vise method of cracking seeds in which the seed is cracked by raising the mandible against the stationary upper jaw. The lateral flange plus the overlying pads of rhamphotheca serve to distribute the shock wave (associated with cracking the seed) evenly to all parts of the upper jaw and the braincase.

c) Variation in the degree of fusion between the palatine process and the palatine: Much variation exists in the degree of fusion between the palatine process of the premaxilla and the palatine and in the development and final degeneration of the isolated splint of bone (= the posterior end of the palatine process), such as seen in the emberizine finches. No sharp break exists between a slightly fused palatine process and a free process, or between a heavily and a completely fused palatine process. Tordoff claimed that the functional basis for this variation in fusion from a free process to a completely fused process is the decrease in size of the *M. pterygoideus*, starting from the cardinal condition. However, in most passerine birds, there is no morphological connection between these two structures; those groups in which part of the *M. pterygoideus* originates from the palatine process have been discussed above. In the emberizine finches, a tendon from the lateral fibers of the *M. pterygoideus* originates on or near the palatine process, but there is not the

simple correlation between the size of this muscle and the fusion of the palatine process as claimed by Tordoff. In fact, the palatine process of the towhee is usually completely fused although this species has a larger lateral tendon of the *M. pterygoideus* than in all other emberizines studied. Therefore, it can be concluded that the variation in the *M. pterygoideus* is not responsible for the variation in the amount of fusion between the palatine process and the palatine.

This variation in the degree of fusion is the result of two quite different factors. Part is doubtlessly the result of a difference in the strength of the primary selection force. It is obvious that there could be a need for a firmer connection between the upper jaw and the palate in some birds and consequently, these birds would have a more heavily fused palatine process. For example, the difference in the fusion of the palatine process in the several genera of woodhewers (*Dendrocolaptidae*) or between *Sapayoa* and the other genera of manakins (*Pipridae*) is probably the result of a difference in the strength of the primary selection force. However, this explanation accounts for only part of the variation. So long as the palatine process fulfills its primary function as an anchorage to which the palatine can fuse, then it does not matter what else happens to it. If the demands of the primary selection force are fulfilled and if there are no other selection forces acting on the palatine process (e.g., for a free process or for a lateral flange), then it would not seem to matter whether the process fuses completely to the prepalatine process, remains partly unfused or starts to degenerate into an isolated splint lying along the prepalatine process. Therefore, I will conclude that, except for the differences in the demands of the primary selection force, there seems to be no functional basis for the variation in the amount of fusion between the palatine process and the palatine, or in the development of the isolated splint. Since this variation in the degree of fusion lies within the limits of the primary selection force, the change from an unfused to a fused process does not appear to be an adaptive change. It would be, however, an evolutionary change, perhaps as pleiotropic expression of a complex gene system.

VARIATION OF THE PALATINE PROCESS OF THE PREMAXILLA

Having ascertained the embryological and the functional significance of the major variants of the palatine process of the premaxilla, it is now necessary to survey its occurrence and

variation throughout the Passeres. In this section, the structure of the palatine process will be recorded, genus by genus, for all but a few families of passerine birds. An attempt was made to separate the observed variation into its separate components — adult, individual, functional and so forth — but it is realized that the conclusions are provisional until good age series and samples of known adults are obtained. These components of variation are the most important part of this survey, and I will summarize them now instead of at the usual place at the end of the section.

The differences in the palatine process between families and occasionally between subfamilies and genera of passerine birds are chiefly functional ones of the type discussed in the preceding section. These variants with their functional interpretation follow.

a) The palatine process unfused to completely fused with the palatine. Slight variants of this series include (a) the anterior end of the process partly degenerate to degenerate, leaving the rest of the process isolated from the premaxilla, and (b) the posterior part of the palatine process fused to the dentary process of the premaxilla and/or to the maxilla. This series represents the stages associated with the varying strength of the primary function of the palatine process which is, of course, to provide a point of anchorage to which the palatine can fuse. When the palatine process fuses to the dentary process of the premaxilla, at least its anterior half fuses to the palatine. The exact reason for the fusion with the dentary process remains, however, unclear. The major problem of this variation in fusion is that it is identical to some aspects of age variation and to non-functional variation in the degree of fusion in the adult; these will be discussed below. No satisfactory means of separating these morphologically similar, but basically different, variants is available. Thus if a series of genera exhibit differences in the degree of fusion between the palatine process of the premaxilla and the prepalatine process, we cannot tell whether the variation is functional, or age variation. However, the differences in the degree of fusion between families, such as that between the heavy-billed icterids and the lighter-billed New World warblers, are frequently functional.

b) The distal end of the palatine process lying free of the prepalatine process and in the space between the palate and the jugal bar. The free process serves as the point of origin for part

of the *M. pterygoideus* which is apparently associated with rapid raising of the mandible.

c) A lateral flange developing at the site of fusion of the palatine process. The flange serves to distribute the shocks associated with cracking of seeds by the vise method employed by the cardueline and other groups of finches.

The variation of the palatine process within a family of passerine birds is commonly quite complex and must be carefully separated into its several components before offering any statements on the variation of the process within the family or the contained genera. Earlier authors (Lucas, 1894, p. 304; Amadon, 1950a, p. 214; and Tordoff, 1954a, p. 23) differ in their opinions on the amount of variation exhibited by the palatine process in a genus of passerine birds. However, their arguments are ambiguous for they did not separate the observed variation into its several components. The following types of variation can be expected when examining the palatine process within a family or genus of passerines.

a) All types of functional variation described above may occur between genera of a family, but they are infrequent. Examples may be: the differences in the fusion of the process in the several genera of woodhewers (*Dendrocolaptidae*) or between *Sapayoa* and the other genera of the manakins (*Pipridae*), or the free process in *Melopyrrha* and *Tiaris* and the lateral flange in *Oryzoborus* as compared to the normal palatine process seen in the other genera of emberizine finches. I do not know of any definite examples of functional differences between congeneric species.

b) Individual variation between adults of a species (or between adults of a genus as recorded in this study) is difficult to ascertain because of the variation in age. There are many examples in which there is no variation between the adults of a genus, usually when the process is completely fused in the adult. If the process is only partly fused in the adult, then it is impossible to determine the adult individual variation without a series of known adults. These were not available. Therefore, I will make the assumption for the purposes of the present study that there is no significant adult variation within genera of passerine birds. This assumption is obviously not correct, but it is very likely not far from the actual condition and it greatly simplifies the study of the minor variations in the degree of fusion between the palatine process and the surrounding bones.

c) The variation resulting from differences in the age of the specimens is of extreme importance because the final adult condition of the palatine process is not reached until the bird is between six months to a year old, because the expression of age variation is very similar to adult individual variation and to certain aspects of functional variation, and because many specimens in skeleton collections are birds less than a year old. Earlier workers have ignored age variation completely and as a consequence, have offered some erroneous conclusions on the amount of individual (adult) and even of functional variation. While examining the specimens used in the survey, I was able to separate some immature birds from adults on the basis of the ossification of the parietal windows and the general ossification of the skeleton, and to compare these groups for differences in the amount of fusion of the palatine process. In general, the palatine process becomes more fused with increasing age. The danger of age variation is that many genera are represented in collections by one or a few specimens so that there is no sure way of determining whether the structure has reached its final adult condition in the bird being examined and hence whether comparisons with other species are proper, i.e., adult with adult and not adult with immature. Realization of the dangers resulting from confusing age variation with adult individual or with functional variation has made me cautious in my discussions of the last two aspects of variation. Consequently, because much of the observed variation in the degree of fusion of the palatine process is the result of differences in the age of the specimens and because fewer erroneous conclusions can be based on age variation, I have assumed that all of the variation in fusion with the exception of obvious cases, such as between the genera of woodhewers, is the result of differences in the age of the specimens. Again, this assumption is possibly wrong, but it is the safest one to use until we have enough good series of specimens of known age.

Methods. The original survey and a major share of the study of the structure and variation of the palatine process of the premaxilla was carried out in the American Museum of Natural History — the entire passerine section of this skeleton collection was utilized. Subsequent study of material in the United States National Museum filled the gaps left after the original survey was completed. All in all, some 3300 specimens representing 500 genera of all but a few passerine families were examined. The missing families are all small groups which do not affect the

overall picture in the Passeres. I believe that an adequate sample of most families, certainly of all the important ones, was obtained. In addition to the Passeres, the Pici and the Coraciæ were examined to acquire an idea of the structure of the palatine process in these groups that are believed to be the nearest relatives of the Passeres.

Only those skulls in which the rhamphotheca of the upper jaw and the membranes in the anterior half of the palate have been removed could be used in the survey. The faint suture separating the palatine process of the premaxilla and, in many cases, the palatine process itself is obscured if there is a thin layer of overlying tissue. A binocular microscope with a magnification of 10x to 15x was used in all examinations.

The structure and variation of the palatine process was determined in each genus available to me. Recording was done on the generic level because, with few exceptions, little or no variation was found between congeneric species; indeed, usually little variation was found between genera of the same family. Also in many cases, the specific identification was lacking or doubtful, and many old names were used so that the task of separating the species and determining the synonymies would have been far greater than justified by the returns. Particular attention was paid to age variation. I tried to assemble a large series of at least one genus in every family, from which the "typical" adult condition of the palatine process and the age variation was determined. The approximate age of the specimens was judged by the general degree of ossification of the skull and especially of the parietal windows (see Chapin, 1949, for a discussion of the parietal windows as a criterion of age in the passerines).

In the following synopsis, the structure of the palatine process is summarized for each family, and in a few cases for the subfamilies, of passerine birds. As mentioned above, the families will be listed according to the sequence to be used in "Peters' Check-list." Under each family (or subfamily) heading, a general description of the palatine process and of its major variation in that family is given. Usually one genus is chosen as the basis for description and comparison in the family. I have tried to choose for this purpose the genus having the most typical palatine process, but this genus is not to be regarded as the type of the family or even as completely typical for that family. If possible, the probable course of ontogenetic development is given. The genera examined are then listed. For each

genus, the number of specimens examined is given in parenthesis and a brief statement of the structure of the process is given. The genera within a family are listed alphabetically rather than according to supposed relationships. A far more complex problem is which generic names should be used. The labels on many specimens bore names no longer used; hence there was the huge task of synonymizing the discarded names with the currently accepted ones. The most convenient solution to this problem was to accept the most recent generic revision of each family. Peters (1951) was followed for the few groups of the suboscines treated in the last volume of his "Check-list." Hellmayr (1924-1938) was consulted for the remaining New World families, and various authors for the Old World groups. In some cases there has not been a recent revision of the family, and for these groups I have used the material in Mayr and Amadon (1951) or have followed the arrangement of genera used in the study collection in the American Museum of Natural History. In any event, the authority followed is cited for each group. I must emphasize that this system is used only because of convenience and not because I may advocate the generic limits set forth by these authors. Nor does it make much difference whether a broad or a narrow generic concept was employed in these revisions; the results of this paper would be the same with either concept.

The schematic drawings accompanying the descriptions (Figs. 23 to 28) show the left half of the upper jaw as seen from below. The arrow points to the palatine process of the premaxilla (labeled "P") or to the region of the fused palatine process. The figures are not drawn to scale.

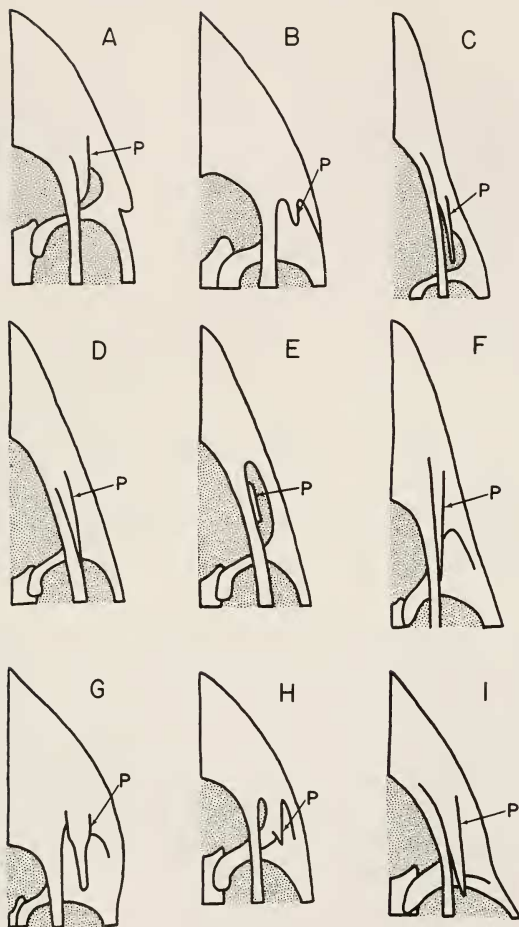


Figure 23. Palatine process of the premaxilla (P) of: (A) *Smithornis* (Eurylaimidae); (B) *Hypocnemis* (Formicariidae); (C) *Furnarius* (Furnariidae); (D) *Formicarius* (Formicariidae); (E) *Formicarius* (Formicariidae); (F) *Agriornis* (Tyrannidae); (G) *Tyrannus* (Tyrannidae); (H) *Cnipodectes* (Tyrannidae); and (I) *Euchlornis* (Cotingidae).

SYNOPSIS OF PASSERINE FAMILIES

Eurylaimidae

The process is present with a varying degree of fusion, from unfused up to the point of being completely lacking (= fused). "Lacking" is a neutral term and will be used when the process is not present as a visible structure, instead of the term "fused" which assumes that the process was present in the embryo and has become fused to the palate. In *Corydon*, the process is present and bears some resemblance to an ossified tendon (of the M. pterygoideus ?). All specimens of *Smithornis* (Fig. 23A) have the process, but the amount of fusion between it and the palate varies greatly. This may, in part, explain the absence of the process in *Calyptomena*, in which I have assumed that the palatine process is fused to the palatine. Lowe (1924) described and figured the palate of *Cymbirhynchus*, *Pseudocalyptomena* and *Smithornis*, but makes no mention of the process. Pycraft (1905a) did not mention the process in *Calyptura*, *Chasmorhynchus*, *Corydon*, and *Cymbirhynchus*, but did say that the anterior process of the palatine is broader where it joins the premaxilla which indicates that the process has fused to the palatines. Thus, it may be concluded that the typical adult condition of the palatine process in the broadbills is for the process to be fused to the palatines and that most, if not all, of the variation observed is because of differences in age and hence the degree of ossification.

Calyptomena (1), lacking; *Corydon* (2), present, somewhat resembles an ossified tendon; *Smithornis* (4), present, amount of fusion varies. Checked with Peters (1951).

Dendrocolaptidae

The process is present in all genera of woodhewers, but the amount of fusion between the process and the palatine varies greatly in the different genera. As a broad generalization, the process is only slightly fused in the long, curved-billed species and heavily fused in those species having a short, straighter and heavier bill. Some of the observed variation may be age, but some is almost certainly correlated with the strength of the bill.

Dendrocincla (2), heavily fused to palatine; *Dendrocolaptes* (1), slightly fused; *Drymornis* (1), slightly fused; *Glyphorhynchus* (2), heavily fused; *Lepidocolaptes* (8), usually slightly fused, but some more fused; *Sittasomus* (2), slightly fused; *Xiphorhynchus* (22), usually slightly fused, but in the medium- to heavy-billed species, the process is as heavily fused as in *Dendrocincla*. Checked with Peters (1951).

Furnariidae

In most genera, the process is present, lying along the palatine and not fused with that bone. In *Furnarius* (Fig. 23C), the process lies free in the space between the palate and the dentary process of the premaxilla and in some ways resembles an ossified tendon. Rarely is the process fused

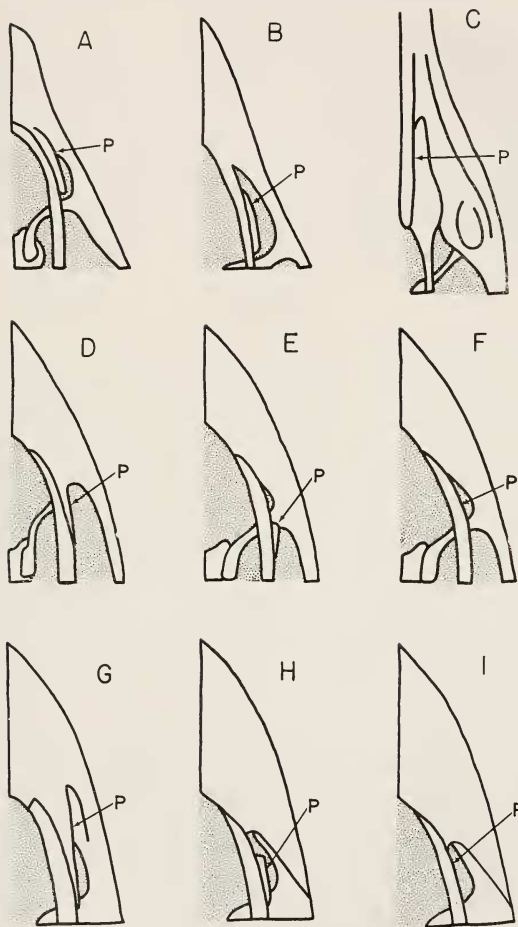


Figure 24. Palatine process of the premaxilla (P) of: (A) *Progne* (Hirundinidae); (B) *Anthus* (Motacillidae); (C) *Acanthorhynchus* (Meliphagidae, redrawn from Parker, 1877); (D) *Spizixos* (Pycnonotidae); (E) *Spizixos* (Pycnonotidae); (F) *Spizixos* (Pycnonotidae); (G) *Garrulax* (Timaliinae); (H) *Garrulax* (Timaliinae); and (I) *Garrulax* (Timaliinae).

or absent as in the case of *Leptasthenura* or *Synallaxis*. The length of the process varies somewhat between the genera.

Anabacerthia (2); *Anumbius* (1); *Aphrastura* (1), lacking ?; *Asthenes* (4); *Automolus* (5); *Chilia* (1), similar to *Furnarius*; *Cinclodes* (1); *Coryphistera* (1); *Cranioleuca* (4); *Furnarius* (22), present, usually lying in the space between the palate and the jugal bars, and reminiscent of an ossified tendon; *Geositta* (5); *Leptasthenura* (5), present, degree of fusion varies greatly; *Lochmias* (1), lacking ?; *Margarornis* (2); *Philydor* (1); *Phleocryptes* (3); *Premnoplex* (1); *Pseudocolaptes* (2); *Pseudoseisura* (2); *Sclerurus* (2); *Schoeniophylax* (1); *Synallaxis* (13), present, varies from unfused to fused; *Upucerthia* (4); *Xenops* (2). Process unfused unless otherwise noted. Checked with Peters (1951).

Formicariidae

The variation of the process in this family is almost as great as that seen in the entire order. In most genera, the process is present, lying along the palatine and scarcely fused to that bone, e.g., *Taraba*. In a few genera, such as *Hypocnemis* (Fig. 23B) and *Cercomacra*, the process lies in the space between the palate and the jugal bar, and seems to fuse, at least in part, with the overlying bone. A considerable amount of variation in the degree of fusion between the process and the palatine exists in some genera, such as *Thamnophilus*, *Phegopsis* and *Myrmorchilus*, in which the process varies from unfused to completely fused with the palatines. In *Formicarius* (Figs. 23D and 23E) the anterior end of the process degenerates until in some individuals only a small isolated splint of bone remains along the palatine. While much of the observed variation in the size and the degree of fusion is the result of age difference and hence of ossification, some of it probably represents true morphological difference between genera. However, no indication of relationships between the genera of the Formicariidae could be determined from the structure of the palatine process.

Cercomacra (5), present, unfused to fused to the palatine; *Chamaeza* (2); *Cymbilaimus* (2); *Dysithamnus* (2); *Formicarius* (5), present, unfused to degenerating at the anterior end to become an isolated splint lying along the palatine; *Formicivora* (7), lacking, no hint in any specimen; *Grallaria* (1); *Gymnopathys* (2); *Herpsilochmus* (1); *Hylophylax* (2); *Hypocnemis* (5) present, rather broad, unfused to fused, lying in the space between the palate and the jugal bar; *Microrhopias* (1) lacking ?; *Myrmeciza* (8), present, as in *Hypocnemis*, or lying next to the palatines; *Myrmorchilus* (2); *Myrmotherula* (6), present, unfused to fused, as in *Hypocnemis*; *Percnostola* (1); *Phaenostictus* (3), present, unfused to fused; *Phegopsis* (1), lacking ?; *Pyriglena* (2); *Sakesphorus* (3); *Taraba* (9); *Thamnophilus* (27), present, unfused to fused. Process unfused unless otherwise noted. Checked with Peters (1951).

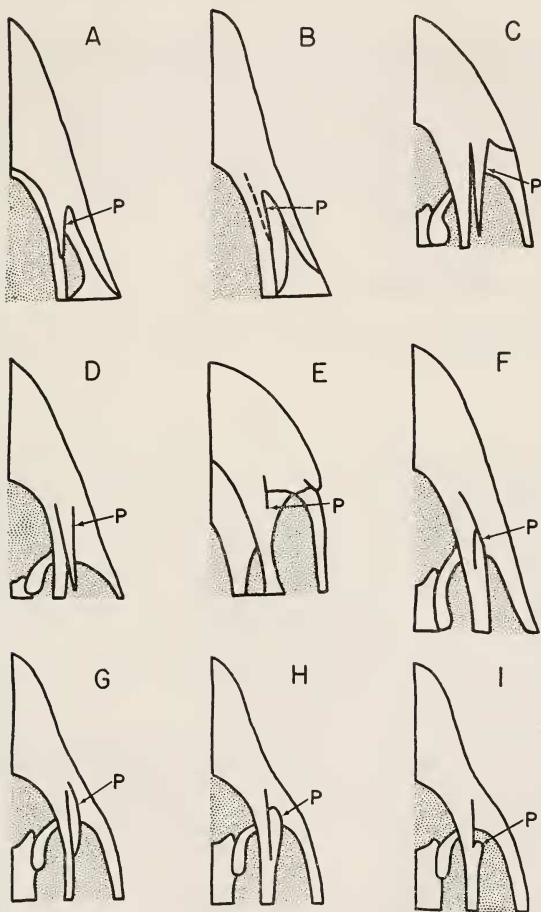


Figure 25. Palatine process of the premaxilla (P) of: (A) *Turdus* (Turdinae); (B) *Turdus* (Turdinae); (C) *Melopyrrha* (Emberizinae); (D) *Tiaris* (Emberizinae); (E) *Oryzoborus* (Emberizinae); (F) *Pipilo* (Emberizinae); (G) *Melospiza* (Emberizinae); (H) *Melospiza* (Emberizinae) and (I) *Melospiza* (Emberizinae).

Conopophagidae

Several specimens of this family were available for study, but unfortunately, the palates of all were damaged. In one skull, a very faint suture on the lateral side of the prepalatine process was seen—an indication that the process may be present, but partly fused with the palatine. Forbes (1881) figured the palate of *Conopophaga* in which the process was not shown. This, however, cannot be accepted as definite evidence that the process is lacking in this family because many authors were unaware of the existence of the process or otherwise failed to mention it.

Rhinocryptidae

The process is universally absent in all specimens examined in this family.

Pterotochos (4); *Rhinocrypta* (1); *Scytalopus* (1). Process lacking. Checked with Peters (1951).

Cotingidae

The process is highly variable in this family; however, it must be remembered that the shape of the bill is also highly variable in the cotingas. The process may be present, but more commonly it is lacking (= fused to the palatine). When present, it usually lies next to the palatine, but in *Euchlornis* (Fig. 23I), it lies free in the space between the palate and the jugal bar. In *Cotinga*, the process may be partly fused to the dentary process of the premaxilla. How much of this variation in the fusion of the process to the surrounding bones is true difference between genera and how much is age variation cannot be determined, but certainly at least some is age. Thus, it is most likely that the adult condition of the palatine process for most genera of this family of broad-billed forms is a completely fused process and that those individuals having an unfused or a partly fused process are immature.

Ampelion (2); *Calyptura* (1); *Cephalopterus* (3); *Cotinga* (1); *Euchlornis* (4), present, long, lying free in the space between the palate and the jugal bar; *Gymnoderus* (1); *Lipaugus* (1); *Pachyramphus* (3), present, unfused in two specimens, fused in the other; *Procnias* (7); *Rupicola* (5); *Tityra* (3). Process lacking unless otherwise noted. Checked with Hellmayr (1929).

Pipridae

The process is present, short and unfused in all genera of this family, except for *Sapayoa* in which it is lacking (= fused). This genus is larger in size than the other manakins and has a broader bill which may account for its completely fused palatine process. This variation is in agreement with the generalization that the process is more fused in those forms with a heavier bill.

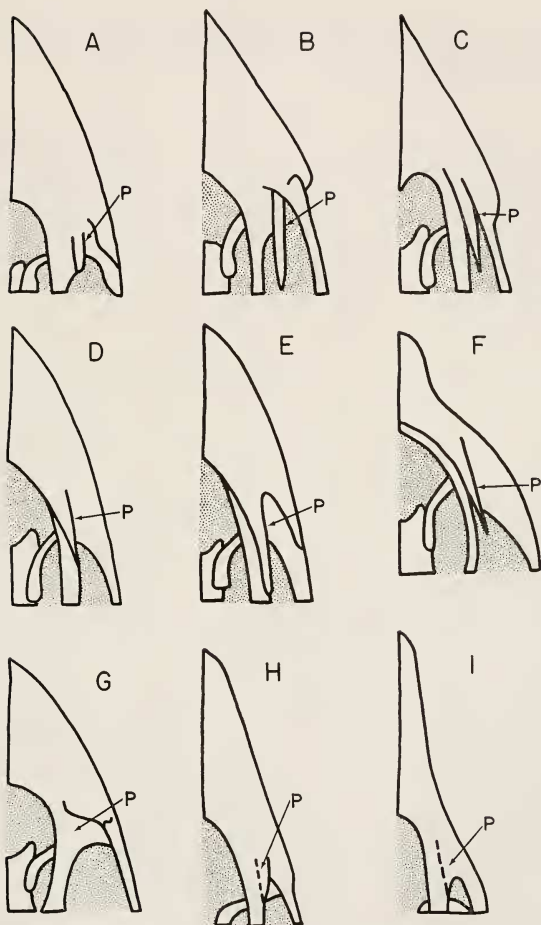


Figure 26. Palatine process of the premaxilla (P) of: (A) *Caryothraustes* (Cardinalinae); (B) *Spiza* (Cardinalinae); (C) *Piranga* (Tanagrinae); (D) *Thraupis* (Tanagrinae); (E) *Buthraupis* (Tanagrinae); (F) *Tersina* (Tersininae); (G) *Psittirostra* (Drepaniidae); (H) *Himatione* (Drepaniidae); and (I) *Vestiaria* (Drepaniidae).

Antilophia (1); *Chiroxiphia* (11); *Corapipo* (1); *Machaeopterus* (1); *Manacus* (4); *Pipra* (18); *Sapayoa* (2), lacking, no hint of the process; *Tyrannetes* (1). Process short and unfused unless otherwise noted. Checked with Hellmayr (1929).

Tyrannidae

The process varies greatly in this family of broad-billed birds. It may be present as a long process lying along the palatine (as in *Agriornis*, Fig. 23F) or as a short process at the base of the palatine (as in *Myiarchus*) or appear as an ossified tendon arising from the mass of bone at the junction between the palatine and the premaxilla or rarely from the maxillo-palatine (as in *Cnipodectes*, Fig. 23H) although it is not absolutely certain whether the short process on the maxillo-palatine is the palatine process), or may be completely absent (as in *Pitangus*). Even within a single genus, such as *Tyrannus*, the process may vary from being present to what appears as a tendinous process arising from the general mass of the premaxilla (Fig. 23G). The commonest condition is for the process to be lacking (= fused) or to vary in the degree of fusion with the palatine, but always with a tendency toward greater fusion. How much of the observed variation is age and how much is difference between genera is impossible to determine at this time. Certainly, at least some of the variation in fusion is age and some is functional.

Agriornis (6), unfused (long-billed form); *Arundinicola* (2); *Blacicus* (1); *Cnemotricus* (7); *Cnipodectes* (1), present, attached to base of the maxillopalatine; *Colonia* (4); *Colopteryx* (4), varies as in *Tyrannus*; *Elaenia* (16), varies as in *Tyrannus*; *Empidonax* (30), usually lacking, but present in a few specimens; *Empidonomus* (3); *Entotricus* (1); *Euscarthmornis* (1); *Fluvicola* (1); *Gubernetes* (1); *Knipolegus* (2); *Legatus* (1); *Lessonia* (4); *Lichenops* (2), lacking in one specimen, present in the other; *Lophotricus* (1); *Mecocerculus* (2); *Megarynchus* (5), varies as in *Tyrannus*; *Muscisaxicola* (2); *Muscivora* (9), varies as in *Tyrannus*; *Myiarchus* (60), varies as in *Tyrannus*; *Myiobius* (1); *Myiochanes* (8), varies as in *Tyrannus*; *Myiophobus* (2); *Myiotheretes* (1), long as in *Agriornis*, *Myiozetetes* (24), varies as in *Tyrannus*; *Nuttallornis* (4); *Ochthoeca* (4); *Ochthornis* (1); *Oncostoma* (1); *Onychorhynchus* (2), varies as in *Tyrannus*; *Phaeomyias* (1); *Pipromorpha* (2) varies as in *Tyrannus*; *Pitangus* (20), varies as in *Tyrannus*, but most have a free process; *Pseudocolopteryx* (1); *Pyrocephalus* (23); *Pyrrhomias* (2); *Rhynchocyclus* (1); *Sayornis* (11); *Serpophaga* (3); *Sirystes* (2), varies as in *Tyrannus*; *Sneathlaga* (1); *Spizitornis* (3); *Sublegatus* (2); *Suiriri* (1); *Todirostrum* (3); *Tolmarchus* (13), varies as in *Tyrannus*; *Tolmomyias* (4); *Tyranniscus* (5), varies as in *Tyrannus*; *Tyrannulus* (1); *Tyrannus* (52), present, to degenerating to what appears as a tendinous process arising from the general mass of bone of the premaxilla (this can be easily broken and is lost in many specimens); *Xolmis* (5), unfused and long in one specimen, lacking in the others. Process lacking unless otherwise noted. Checked with Hellmayr (1927).

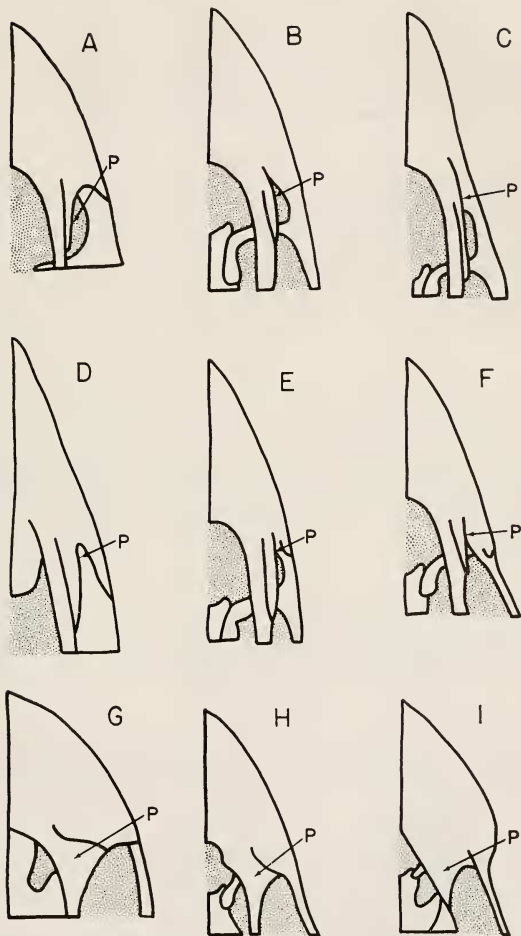


Figure 27. Palatine process of the premaxilla (P) of: (A) *Virco* (Vireonidae); (B) *Icteria* (Parulidae); (C) *Euphagus* (Icteridae); (D) *Gymnostinops* (Icteridae); (E) *Quiscalus* (Icteridae); (F) *Fringilla* (Fringillinae); (G) *Coccothraustes* (Carduelinae); (H) *Carduelis* (Carduelinae); and (I) *Lonchura* (Estrildidae).

Oxyruncidae

One badly preserved specimen was available for study. The process is apparently lacking, but because of the condition of the specimen, there is still some question as to the true condition of the process.

Oxyruncus (1), lacking ?. Checked with Hellmayr (1929).

Phytotomidae

The process is absent in all specimens of this monotypic family and may be fused, at least in part, with the dentary process of the premaxilla instead of with the palatine. *Phytotoma* is a heavy-billed bird so that its fused process provides additional evidence for the generalization that the process fuses completely with the surrounding bones in heavy-billed birds.

Phytotoma (9), lacking (fused with the dentary process of the premaxilla ?). Checked with Hellmayr (1929).

Pittidae

The process is present, but varies from being partly fused to completely fused with the palatine. The bill is approximately the same shape and size in all specimens, therefore this variation is most likely age and not the result of functional differences. Consequently, the typical adult condition is assumed to be a completely fused process and those specimens with a partly fused process are probably immature birds.

Pitta (18), unfused in 11 specimens, lacking in the other 7. Checked with Peters (1951).

Xenicidae

No specimens of this rare family were available for study. Forbes (1882) did not mention this process in his paper on the anatomy of *Xenicus* and *Acanthisitta*. Pycraft (1905b) described and figured the palate of *Acanthisitta*, but also did not mention the process.

Philepittidae

No specimens of this family were available for study. Forbes (1880) reported on the anatomy of *Philepitta* and figured the palate in which the process was not shown.

Menuridae

The process is lacking in this group of large birds with relatively heavy bills.

Menura (2), lacking. Checked with Mayr and Amadon (1951).

Atrichornithidae

No specimens of this rare family were available for study. The only anatomical study of *Atrichornis* that I know of is by Garrod (1877), but unfortunately he does not describe the palate.

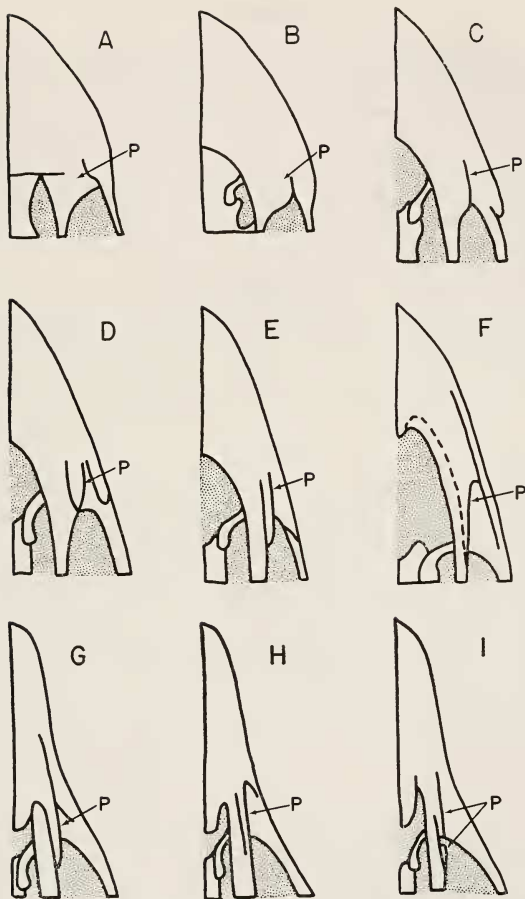


Figure 28. Palatine process of the premaxilla (P) of: (A) *Spermospiza* (Estrildidae); (B) *Ploceus* (Ploceidae); (C) *Passer* (Ploceidae); (D) *Dinemellia* (Ploceidae); (E) *Bubalornis* (Ploceidae); (F) *Cyanocitta* (Corvidae); (G) *Paradisaca* (Paradisaeidae); (H) *Paradisaca* (Paradisaeidae); and (I) *Paradisaca* (Paradisaeidae).

Alaudidae

The process is present in most genera of larks, but there is much variation in the degree of fusion between it and the palatine. In some genera, such as *Eremophila*, the process is completely lacking (= fused). When present, the process usually lies along the palatine, but in *Melanocorypha*, it lies free in the space between the palate and the jugal bar. *Certhilauda* has a long, decurved bill and lacks the process. This is the opposite of the condition found in many groups in which the heavy-billed forms lack the process and the species with long, thin or decurved bills have a well-developed process. However, *Certhilauda* uses its bill to dig in the ground (Meinertzhagen, 1951, p. 101) and the fused process probably gives the bill greater strength as in the thrashers (*Torostoma*).

Alauda (8), degree of fusion varies; *Calandrella* (1), process almost completely fused with the palatine and the jugal bar; *Certhilauda* (1), lacking; *Eremophila* (17), lacking; *Eremopterix* (3), unfused; *Lullula* (1), lacking; *Melanocorypha* (1), process lying free in space between the palate and the jugal bar; *Mirafr*a (5), partly fused to the palatine. Checked with Vaurie (1951) and Meinertzhagen (1951).

Hirundinidae

Most genera of swallows have a well-developed process which lies next to the palatine and is not fused at all with that bone (Fig. 24A). In *Iridoprocne*, the degree of fusion varies from unfused to completely fused with the palatine. All specimens of *Hirundo* lacked the process. The bill of all genera of swallows is equally broad and apparently similar in function so that the significance of the variation in *Iridoprocne* and *Hirundo* remains a mystery.

Atticora (2); *Delichon* (4); *Hirundo* (22), lacking; *Iridoprocne* (20), present, but varies from unfused to completely fused; *Lamprochelidon* (1); *Orochelidon* (1); *Petrochelidon* (6); *Phacoprogne* (2); *Progne* (14); *Riparia* (5); *Stelgidopteryx* (10); *Tachycineta* (2). Process present and unfused unless otherwise noted. Checked with Hellmayr (1935) and with Mayr and Bond (1943).

Motacillidae

In this family of thin-billed species, the process is lost except for a thin isolated splint of bone lying along the palatines in some specimens (Fig. 24B). This splint can be easily broken off, so that it is not known how much of the observed variation is natural and how much is artificial.

Anthus (36), usually lacking, but in a few specimens there is an indication of an isolated splint lying along the palatine; *Macronyx* (3), isolated splint in one specimen, lacking in the others; *Motacilla* (33), lacking or present as a splint lying along the palatine. Checked against the A.M.N.H. collection.

Campephagidae

In a few genera of the cuckoo-shrikes, such as *Campephaga*, there is a short process at the anterior end of the palatines. In most genera, however, the process fuses to the palatines. This seems to be the typical adult condition in this family and the observed variation in fusion appears to be age variation.

Campephaga (4), short, unfused; *Coracina* (8), lacking; *Edolisoma* (2), lacking; *Hemipus* (2), lacking; *Lalaga* (1), present (?), short; *Pericrocotus* (43), lacking, but in a few specimens there is a hint of a process; *Volvocivora* (1), short, partly fused. Checked against the A.M.N.H. collection.

Pycnonotidae

The process varies from being present and unfused to completely fused in the bulbuls. In general, it fuses partly to the prepalatine process to form a large part of that bone and partly to the dentary process of the premaxilla. In a few genera, such as *Spizixos* (Figs. 24D, 24E, and 24F), the process degenerates at its anterior end to become a thin, isolated splint of bone lying along the palatine, such as in *Paradisaca* or in *Motacilla*. Except for the difference between the *Microscelis*-type and the *Spizixos*-type, the variation in the degree of fusion between the process and the palatine is probably age variation; the difference between *Spizixos* and *Microscelis* is probably functional, but more than that I cannot say.

Baeopogon (4); *Bleda* (5); *Calyptocichla* (2); *Criniger* (6); *Ixonotus* (1), lacking ?; *Microscelis* (33); *Phyllastrephus* (4); *Pycnonotus* (93); *Spizixos* (26), present, the anterior end generally degenerating to an isolated splint lying along the palatine; *Thescelocichla* (2); *Trachycomus* (5). Unless otherwise stated, the process varies from unfused to fused with the prepalatine process and, in part, to the dentary process of the premaxilla. Checked with Delacour (1943a).

Irenidae

The nature and variation of the process in this family is identical to that in the closely related Pycnonotidae.

Aegithina (8), partly fused to completely fused with the palatine; *Chloropsis* (8), lacking; *Irena* (8), partly fused to completely fused with the palatine. Checked with Mayr and Amadon (1951).

Laniidae

The process is lacking (= fused) in most members of this heavy-billed family. A few specimens, however, have a small, partly fused process at the anterior end of the palatine, which indicates that the process fuses with the palatine and that any variation is probably due to age.

Dryoscopus (6), lacking; *Laniarius* (13), lacking, one specimen had a faint suture showing that the process had fused to the palatine; *Lanius*

(13), partly fused to completely fused; *Malacotus* (3) lacking; *Pelicanus* (1), long, partly fused to the palatine; *Rhodophoneus* (1), lacking; *Tachagra* (3), one specimen had a long, partly fused process, the other lacked the process; *Urolestes* (2), lacking. Checked against the A.M.N.H. collection.

Prionopidae

No specimens of this family were available for study, nor could I find a description of the palate in the literature. It is most likely that they agree with the Laniidae in the structure of the process. Genera checked with Mayr (1943).

Vangidae

No specimens of the vanga shrikes were available for study, nor could I find a description of their palate in the literature. It is most probable that the structure of the process in the vangids is the same as in the true shrikes.

Bombycillidae

The process is lacking in all but a few specimens of this family. These latter specimens, especially the two individuals of *Dulus*, are probably immature birds in which the process is less fused to the palatine. As in the preceding families, the observed variation is the result of a difference in age and hence in ossification.

Bombycilla (33), lacking or a faint indication in a few specimens; *Dulus* (10), usually lacking, but two specimens had a well-developed process; *Phainopepla* (9), lacking; *Ptilogonys* (5), lacking. Checked with Mayr and Amadon (1951) and with Delacour and Amadon (1949).

Cinclidae

As in the closely related thrushes, the process in the dipper is lacking as a distinct structure in the adult and is assumed to be fused with the palatine.

Cinclus (7), lacking. Checked with Mayr and Amadon (1951).

Troglodytidae

Most specimens examined lacked a process; however, in a few genera, such as *Heleodytes*, *Cinnycerthia* and *Thryothorus*, the process varies from being present, but partly fused, to completely fused with the palatine. It appears that the adult condition is complete fusion and that the observed variation is due to age.

Catherpes (2); *Cinnycerthia* (8), varies as in *Heleodytes*; *Cistothorus* (4); *Heleodytes* (15), partly fused to completely fused with the palatine; *Henicorhina* (1); *Leucoclepis* (1); *Salpinctes* (6); *Thryomanes* (1); *Thryothorus* (55), varies as in *Heleodytes*; *Troglodytes* (31). Process lacking unless otherwise noted. Checked with Hellmayr (1934).

Mimidae

Except for *Margarops*, the process is lacking (= fused) or heavily fused with the palatine in all genera of the mimids. Individuals having a partly fused process are, with little doubt, immature birds and the variation in the degree of fusion is thus due to age. In the case of *Margarops*, however, it seems likely that the process is present and not fused to the palatine in the adult bird (that is, the four birds examined are not immature), but the significance of this difference between *Margarops* and the rest of the mimids is not known.

Alcenia (2); *Cinclocerthia* (1); *Donacobius* (1); *Dumetella* (13), a hint of the process in a few specimens, and in one specimen the process was only slightly fused; *Margarops* (4), unfused, lying next to the palatine, *Melanoptila* (1); *Melanotis* (3); *Mimodes* (1); *Mimus* (7); *Nesomimus* (3); *Oreoscoptes* (2); *Toxostoma* (8). Process lacking unless otherwise noted. Checked with Hellmayr (1934).

Prunellidae

The process is lacking in *Prunella* as in the closely related Turdinae. *Prunella* (5), lacking. Checked with Marien (1951).

Turdinae

The process is usually fused to one or more of the surrounding bones (the palatine or the dentary process of the premaxilla). In a few genera, such as *Hylocichla* or *Turdus*, a partly fused process is present in some specimens which are assumed to be young birds (Fig. 25A and 25B). Hence, the fused process is the adult condition and any variation in the degree of fusion is mostly likely due to differences in age.

Alethe (4); *Callene* (2); *Cichladusa* (18); *Copsychus* (18); *Cossypha* (5); *Enicurus* (12); *Erithacus* (31); *Erythropygia* (1); *Hylocichla* (18), a faint indication of the process in a few specimens; *Monticola* (1); *Myadestes* (3); *Necocossyphus* (2); *Oenanthe* (4); *Phaeornis* (1); *Phoenixurus* (16); *Saxicola* (25); *Sialia* (15); *Thamnolaea* (2); *Turdus* (19), a faint indication of the process in a few specimens and a partly fused process in two others; *Zoothera* (2). Process lacking unless otherwise noted. Checked with Ripley (1952).

Timaliinae

The variation of the process in either *Garrulax* (Figs. 24G, 24H, 24I) or *Liothrix* is typical for this subfamily. In these genera, the process varies from being present and unfused to fused with any of the surrounding bones (palatine, or the dentary process of the premaxilla). The adult condition is thus assumed to be a completely or an almost completely fused process and the observed variation in the degree of fusion to be due to age.

Alcippe (19), varies as in *Liothrix*; *Babax* (4), varies as in *Garrulax*; *Chamaea* (5), lacking; *Chrysomma* (1), unfused, lying along the palatine; *Dumetia* (1), fused to dentary process of the premaxilla; *Gampsorhynchus* (1), fused to dentary process of the premaxilla; *Garrulax* (55), unfused to fused with the dentary process of the premaxilla, process also partly overlies the palatine; *Heterophasia* (3), fused to the dentary process; *Lioptila* (4), varies as in *Liothrix*; *Liothrix* (38), long and unfused, with the anterior end fusing to the dentary process, and thus leaving an isolated splint of bone (the posterior end of the process) lying along the palatine; *Macronus* (4), fused to the dentary process; *Malaccincla* (5), varies as in *Garrulax*; *Malia* (1), varies as in *Garrulax*; *Pellorneum* (1), fused to the dentary process; *Pomatorhinus* (7), varies as in *Liothrix*; *Psophodes* (2), varies as in *Garrulax*; *Pteruthius* (5), varies as in *Garrulax*; *Rhinocichla* (1), heavily fused to the palatine; *Siva* (10), varies as in *Liothrix*; *Stachyris* (6), varies as in *Liothrix*; *Trochalopteron* (25), varies as in *Garrulax*; *Turdoides* (2), varies as in *Garrulax*; *Yuhina* (26), varies as in *Liothrix*. Checked with Delacour (1946).

Paradoxornithinae

The process is lacking in the one genus examined in this subfamily and it is assumed to be fused as in the closely related Timaliinae.

Suthora (5), lacking. Checked with Delacour (1946).

Polioptilinae

The process is lacking (= fused) in this group of thin-billed birds and is similar to that seen in the closely related Sylviinae.

Microbates (4), lacking, but with a hint of a fused process; *Polioptila* (10), lacking; *Ramphocaenus* (1), lacking. Checked with Rand and T aylor (1953).

Sylviinae

The process is lacking (= fused) in almost all genera of this subfamily. In a few genera, such as *Cisticola* and *Prinia*, an unfused process is present in some specimens. This indicates that the typical adult condition is for the process to be fused with the palatine and that the observed variation in the degree of fusion is age variation.

Abroscopus (3); *Acrocephalus* (9); *Apalis* (2); *Bradornis* (5), (may be a musciapiine?); *Camaroptera* (2); *Cisticola* (9), present as a long thin process that is partly or completely fused to the palatine; *Eremomela* (2), present in one specimen, lacking in the other; *Franklinia* (3); *Hylia* (1); *Hypergerus* (2); *Oreopneuste* (1); *Phragamaticola* (1); *Phylloscopus* (23), a small splint of bone lying along the palatine in one specimen, signs of a fused process in a few other specimens; *Prinia* (10), present, small, at the very anterior end of the palatine, partly fused in two specimens; *Regulus* (27); *Seicercus* (1); *Sylvia* (6); *Sylvietta* (2); *Tribura* (8); *Urosphena* (1). Process lacking unless otherwise noted. Checked against the A.M.N.H. collection.

Malurinae

The process is lacking in the Malurinae.

Malurus (1), lacking. Checked with Mayr and Amadon (1951).

Muscicapinae

The process is almost universally lacking in the Old World flycatchers, but there is a hint of a process in a few specimens, e.g., *Culicicapa*, which indicates that the broad anterior end of the palatine process is composed in part of the fused process. Thus the adult condition is for the process to be fused and any variation in fusion is most likely age variation.

Batis (2); *Bias* (2); *Culicicapa* (5), hint of a fused process in one specimen; *Erranornis* (2); *Erythrocercus* (1); *Ficedula* (11); *Fraseria* (2); *Hyliota* (1); *Muscicapa* (10); *Niltava* (4); *Platysteira* (1). Process lacking. Checked with Vaurie (1953) and against the A.M.N.H. collection.

Monarchinae

The process is lacking as in the closely related Muscicapinae.

Chasiempis (1); *Hypothymis* (7); *Terpsiphone* (11); *Trochocercus* (2). Process lacking. Checked with Mayr and Amadon (1951) and against the A.M.N.H. collection.

Pachycephalinae

The process is lacking in this group of heavy-billed flycatchers.

Colluricincla (2); *Eopsaltria* (1); *Falcunculus* (1); *Pachycephala* (4). Process lacking. Checked with Mayr and Amadon (1951) and against the A.M.N.H. collection.

Paridae

A short process is present in some individuals which becomes fused, in part with the dentary process of the premaxilla, but mainly with the palatine in the adult. The variation in the degree of fusion is assumed to be age and hence ossification.

Aegithaliscus (3); *Aegithalos* (2); *Parus*, a partly fused process is present in a few specimens; *Psaltriparus* (6). Process lacking. Checked with Mayr and Amadon (1951) and against the A.M.N.H. collection.

Sittidae

The process is lacking in all specimens of this heavy-billed family. However, in one specimen of *Sitta*, there is a suggestion of a suture on the prepalatine process indicating that the process has fused with the palatine.

Rhabdornis (1); *Sitta* (49); *Tichodroma* (1). Process lacking. Checked with Mayr and Amadon (1951).

Certhiidae

The process is lacking (= fused) in most specimens of this thin-billed genus, this being the typical adult condition. In one specimen, however, the process is only partly fused to the palatine which indicates that the process is present and unfused in the immature and becomes increasingly fused with age.

Certhia (17), lacking, but a slight indication of the process in one specimen. Checked with Mayr and Amadon (1951).

Dicaeidae

The typical condition of the process in this thin-billed family is a thin isolated splint lying along the palatine. In some specimens, presumably immatures, the process is still attached to the premaxilla. In others, the anterior connection to the premaxilla has degenerated toward the typical adult condition. If the process is lacking, it is most likely the result of loss during preparation, although the process could degenerate completely in some specimens.

Dicaeum (7), lacking or as a splint lying along the palatine. Checked with Mayr and Amadon (1947).

Nectariniidae

The process is usually lacking in this family of long, thin-billed birds. In a few specimens, there is a slight suggestion that the process has become fused to the palatine during development.

Aethopyga (3); *Anthreptes* (2); *Arachnothera* (2); *Nectarinia* (23), a slight indication of the process in a few specimens. Process lacking. Checked with Delacour (1944).

Zosteropidae

The process is usually lacking in this family of short thin-billed species with the usual indication of a semifused process in a few specimens.

Zosterops (15), usually lacking. Checked with Mayr and Amadon (1951).

Meliphagidae

The process is lacking (= fused) in most specimens of this family. In *Philemon*, however, the process is present, but at least partly fused to the palatine. Thus it is evident that in the adult of this family, the process fuses to the prepalatine process and that any variation in fusion is probably due to age.

Parker (1877) reported that the palatine process in *Acanthorhynchus* (Fig. 24C) lies along the medial side of the palatine. This is possible, although the specimen of the genus that I examined did not show this

condition. I was careful to check specimens of the entire order for additional examples in which the palatine process lay on the inside rather than on the outside of the palatine, but could not find any such specimens. Thus, I would suggest that the palatine process in *Acanthorhynchus* is normal and lies on the lateral side of the palatine.

Acanthorhynchus (1); *Conopophila* (1); *Melilestes* (1); *Meliornis* (2); *Meliphaga* (2); *Melithreptus* (2); *Myzantha* (1); *Myzomela* (3); *Philemon* (6), present, but partly fused to the palatine. Process lacking unless otherwise noted. Checked against the A.M.N.H. collection.

Emberizinae

The process varies greatly in this group of finches. Typically, it lies next to the palatines and is more or less fused to that bone, but in a number of specimens, it is completely fused (Fig. 25F). The figures of *Melospiza melodia* (Figs. 25G, 25H, and 25I) illustrate what seems to be the typical course of reduction and fusion of the process with increase in age; however, the process can also fuse to the palatine without any reduction in size. In *Melopyrrha* (Fig. 25C) and *Tiaris* (Fig. 25D), the process lies free in the space between the palate and the jugal bar and appears similar to that seen in the cardinals. In *Oryzoborus* (Fig. 25E), a very heavy-billed species, the process is completely fused to the palatine and in its place is a lateral flange similar to that seen in the Carduelinae. Much of the observed variation in this family is no doubt age variation, but aside from *Melopyrrha*, *Tiaris*, and *Oryzoborus* which are special problems, it is difficult to determine the fully adult condition in the different genera. Hence the significance, both taxonomically and functionally, of the variation in fusion cannot be evaluated at this time.

Ammospiza (7), unfused to almost completely fused; *Arremonops* (1), lacking; *Calcarius* (1), lacking ?; *Emberiza* (6), slightly fused; *Gubernatrix* (4), slightly fused; *Junco* (8), slightly fused; *Melopyrrha* (2), lying free in the space between the palate and the jugal bar; *Melospiza* (16), slightly fused to completely fused, specimens show reduction of the anterior end of the process; *Oryzoborus* (3), lacking, anterior end of palatine has a lateral flange; *Paroaria* (10) slightly fused to almost completely fused; *Passerculus* (9), partly fused to completely fused; *Passerella* (7), lacking, some specimens with a faint suture; *Phrygilus* (1), slightly fused; *Pipilo* (9), partly fused to completely fused; *Plectrophenax* (7), slightly fused; *Pooecetes* (1), lacking; *Sicalis* (1), lacking; *Spizella* (7), slightly to partly fused; *Sporophila* (7), lacking, one specimen showed a hint of the process; *Tiaris* (1), free as in *Melopyrrha*; *Zonotrichia* (15), slightly fused. Checked with Tordoff (1954a).

Cardinalinae

The process is present in all genera of this heavy-billed group of finches. Usually it lies free in the space between the palate and the jugal bar (Figs. 3 and 26B), but in some genera, such as *Caryothraustes*

(Fig. 26A) and *Saltator*, the process lies along the palatines. There may or may not be a suture between the free process and the rest of the premaxilla, but the process never fuses to the palatine. At the present time, none of the observed variation can be correlated with any functional or taxonomic significance.

Cardinalis (14), free; *Caryothraustes* (1), lying along the palatine; *Guiraca* (3), free; *Passerina* (7), free; *Pheucticus* (9), free; *Saltator* (8), in some specimens it lies free, in others it lies along the palatine; *Spiza* (1), free (may be *icterid*). Checked with Tordoff (1954a).

Tanagrinae

The process is present in all specimens of tanagers that were examined. It may lie in the space between the palate and the jugal bar, but usually it lies along the palatine although the two bones apparently do not fuse (Figs. 26C, 26D, and 26E). A suture separating the process from the rest of the premaxilla may or may not be present. Tordoff reports the process as being partly fused to the palatine with a suture present; this does not agree with my findings that the process does not fuse at all with the palatine. However, because of the difficulty of determining the degree of fusion between the process and the palatine by examination of the ventral aspect of the palate, this difference of interpretation is of no importance.

Buthraupis (1); *Calospiza* (9); *Chlorophonia* (1); *Chlorospingus* (1), lying free; *Compsocoma* (1); *Habia* (1); *Hemithraupis* (1); *Orthogonys* (1); *Poecilothraupis* (2); *Pipraeidea* (2); *Piranga* (9), lying free; *Ramphocelus* (2); *Schistochlamys* (3); *Spindalis* (2); *Tachyphonus* (3); *Tangara* (21); *Tanagra* (8). Process present, unfused or free. Checked with Hellmayr (1936).

Tersininae

The process is present in this swallow-billed species. It lies somewhat free in the space between the palate and the jugal bar, but still closely attached to the palatine (Fig. 26F). In general, the process resembles that seen in the true swallows.

Tersina (3), unfused, lying somewhat free. Checked with Hellmayr (1936).

Coerebinae

The process is present in this group of thin-billed birds. It always lies against the palatine, but its length varies as does the degree of fusion with the palatine, which varies from slightly fused to completely fused. How much of the variation in the degree of fusion is age variation and how much represents a true difference between genera is unknown.

Ateleodacnis (4), heavily to completely fused; *Chlorophanes* (3), long, slightly to completely fused; *Coereba* (12), short, partly to completely fused; *Conirostrum* (2), long, slightly fused; *Cyanerpes* (24), long, slightly

(usually) to heavily fused; *Dacnis* (4), slightly to strongly fused; *Diglossa* (3), long, partly fused; *Eumcornis* (2), short, not fused. Checked with Hellmayr (1935).

Catamblyrhynchinae

The process is lacking (= fused) in this heavy finch-billed genus. *Catamblyrhynchus* (2), lacking. Checked with Hellmayr (1938).

Parulidae

In this family of thin-billed birds, the process is present as a thin splint lying along the palatine (Fig. 27B). It degenerates at its anterior end and becomes fused to the palatine with increasing age. The fully adult condition is apparently for the process to be heavily fused with the palatine; hence the observed variation in fusion is most probably age variation.

Dendroica (79); *Geothlypis* (8); *Helmitheros* (3); *Icteria* (4); *Mniotilta* (12); *Parula* (2); *Protonotaria* (2); *Oporornis* (10); *Seiurus* (34); *Setophaga* (10); *Vermivora* (13); *Wilsonia* (10). Process present, lying along the palatine with the anterior end degenerating to leave a thin splint which finally fuses with the palatine. Checked with Hellmayr (1935).

Drepaniidae

In the heavy, finch-billed genus, *Psittirostra* (Fig. 26G), the process and the anterior half of the palate is exactly like that in the cardueline finches. In the other genera, the process is lacking (= fused), but the anterior end of the palatine does not flare out to the side as strongly as in *Psittirostra*, and in some there is no flaring of the palatine (Figs. 26H, and 26I). In at least one specimen, that of *Hemignathus*, a faint suture is present on the lateral half of the prepalatine process, which indicates that the process is present, but has fused completely to the palatine.

Hemignathus (1), long, curved-bill; *Himatione* (3), short, medium-bill; *Loxops* (1), short, thin-bill; *Psittirostra* (9), lateral flange present, bill similar to cardueline bill; *Vestiaria* (1), medium, curved-bill. Process lacking. Checked with Amadon (1950a).

Vireonidae

The process is lacking (= fused) in all specimens of vireos (Fig. 27A), except for one in which the process is visible but heavily fused to the palatine. This indicates that the process is present in the immature and becomes fused with the palatine with increasing age. The process is lacking in *Cyclarhis*, a heavy-billed species. I was unable to examine any specimen of *Vireolanus*, another heavy-billed species, but presumably the process of this genus would be similar to that seen in *Vireo* and *Cyclarhis*.

Cyclarhis (7), lacking; *Vireo* (16), lacking in all but one specimen which showed a faint suture. Checked with Hellmayr (1935).

Icteridae

The process is lacking (= fused) in most specimens examined in this family. In some specimens, however, e.g., *Euphagus*, *Gymnomystax*, *Icterus*, *Xanthornus* and *Quiscalus*, the process is absent, but usually heavily fused with the palatine (Figs. 27C, 27D, and 27E). This variation is, no doubt, mainly due to differences in age; the adult condition is presumed to be complete fusion between the process and the palatine.

Agelaius (6), suture sometimes weakly present; *Amblycercus* (2); *Cacicus* (3); *Dolichonyx* (4); *Euphagus* (3), present, slightly fused to almost completely fused; *Gnorimopsar* (1); *Gymnomystax* (2), suture very faint; *Gymnostinops* (2); *Holoquiscalus* (1), with a faint suture; *Hypopopyrrhus* (1), present, but heavily fused; *Icterus* (22); heavily fused in some specimens; *Molothrus* (7); *Notiopsar* (2); *Pezites* (3); *Psomocolax* (1); *Quiscalus* (15), heavily fused in some specimens; *Sturnella* (6), suture sometimes weakly present; *Tangavius* (1); *Xanthocephalus* (1); *Xanthornus* (1), faint suture; *Zarhynchus* (1). Process lacking unless otherwise noted. Checked with Hellmayr (1937).

Fringillinae

In *Fringilla*, the process is present and lies along the palatine, much the same as that seen in many genera of the Emberizinae. However, it may be even less fused with the palatine than in that group (Fig. 27F).

Fringilla (3), present, slightly fused, lying along the palatine. Checked with Mayr *et al.* (1956).

Carduelinae

The process is lacking (= fused) in all specimens of this group of heavy-billed finches. In addition, the anterior end of the prepalatine process bears a lateral flange (Figs. 4, 27G, and 27H).

Carduelis (including *Acanthis* and *Spinus* specimens) (18); *Carpodacus* (14); *Chloris* (3); *Coccothraustes* (3); *Eophona* (2); *Hesperiphona* (19); *Leucosticte* (6); *Loxia* (6); *Pinicola* (3); *Polioptila* (2); *Pyrrhula* (1); *Serinus* (12). Process lacking, but lateral flange present. Checked with Mayr and Amadon (1951) and against the A.M.N.H. collection.

Estrildidae

All specimens examined had a lateral flange similar to that in the Carduelinae (Figs. 27I, and 28A). As in that group, it is assumed that the process has fused with the palatine to form part of the lateral flange.

Amadina (4); *Clytopiza* (1); *Erythrura* (2); *Estrilda* (14); *Lonchura* (16); *Poephila* (11); *Pytilia* (3); *Pyrenestes* (1); *Spermophaga* (1); *Steganopleura* (4). Process lacking, but lateral flange present. Checked with Delacour (1943b).

Bubalornithinae

The process is present in *Bubalornis* and *Dinemellia* (Figs. 28D, and 28E) as reported earlier by Sushkin (1927). In these genera, the process lies next to the palatine and is partly fused with that bone.

Bubalornis (1), present, but heavily fused; *Dinemellia* (3), present, lying next to the palatine, slightly to partly fused.

Passerinae

The process is usually lacking (= fused) in this subfamily (Fig. 28C). It may be present in some specimens as a heavily fused process, but the sutures are so faint that it is difficult to determine their true nature.

Passer (15), lacking.

Ploceinae

The process is lacking in this subfamily of weaver finches. The anterior part of the prepalatine process flares out to the side as in the carduelines.

Anaplectes (1); *Coliuspasser* (3); *Diatropura* (2); *Euplectes* (9); *Malimbus* (1); *Plocepasser* (2); *Ploceus* (7); *Pseudonigrita* (1); *Sporopipes* (1). Process lacking, but lateral flange present.

Viduinae

The process in the widow birds is the same as that in the Ploceinae, but except for *Hypochera*, they lack the lateral flange.

Hypochera (1), lacking, flange present; *Steganura* (1), lacking, flange absent; *Vidua* (2), lacking, flange absent. Subfamilies of Ploceidae follow Tordoff (1954a), genera checked with Chapin (1917) and against the A.M.N.H. collection.

Sturnidae

The process is lacking (= fused) in almost all specimens of starlings examined. In a few specimens of *Sturnus*, a faint suture could be seen which suggests that the process is present in the immature and becomes fused with increasing age.

Acridotheres (2); *Creatophora* (1); *Lamprotornis* (4); *Mino* (2); *Onychognathus* (2); *Spreo* (8); *Sturnus* (11), hint of process in a few specimens. Process lacking. Checked with Amadon (1943).

Oriolidae

The process is lacking (= fused) in most specimens of this family. In a few specimens of *Oriolus*, a faint suture can be seen which indicates that the process is present in the immature and becomes fused with age.

Oriolus (23), present, but partly fused in five specimens, lacking in the rest; *Sphecothebes* (3), lacking. Checked against the A.M.N.H. collection.

Dieruridae

The process is lacking (= fused) in all specimens of drongos.

Dicrurus (39), lacking. Checked with Vaurie (1949).

Callaeidae

The process is lacking (= fused) in all specimens of this family.

Callaeas (1), lacking, heavy-billed form; *Neomorpha* (1, female), lacking, long, curved-billed species (the palatine process is not shown in the figure of the palate of the male [Garrod, 1872], which has a much shorter and stouter bill); *Philesturnus* (1), lacking, short slender bill. Checked with Stonor (1942).

Grallinidae

The process is lacking (= fused) in all specimens of *Corcorax* and *Grallina*, but present in *Struthidea*. This apparently represents a true difference between these genera which may be a reflection of the possible artificial nature of this family.

Corcorax (1), lacking; *Grallina* (8), lacking; *Struthidea* (4), present, lying along the palatine. Checked with Amadon (1950b).

Artamidae

The process is lacking (= fused) in this broad-billed, swallow-like genus, but in some specimens there is an indication that the process has fused with the palatine.

Artamus (7), lacking, but a faint indication in a few specimens. Checked with Mayr and Amadon (1951).

Cracticidae

The process is lacking (= fused) in all specimens examined in this family.

Cracticus (1); *Gymnorhina* (7); *Strepera* (3). Process lacking. Checked with Amadon (1951).

Ptilonorhynchidae

The process is lacking (= fused) in almost all specimens of the bowerbirds. Its presence in one specimen of *Ailuroedus* indicates that the process has fused to the palatine and that any variation in fusion is age variation.

Ailuroedus (5), present in one specimen; *Chlamydera* (2); *Ptilonorhynchus* (9); *Xanthomelus* (1). Process lacking. Checked against the A.M.N.H. collections.

Paradisaeidae

The process varies greatly in the birds of paradise. In most genera, it is lacking or heavily fused to the palatine. In a few genera, such as *Manucodia*, a quite distinct process is present in some specimens. In

Paradisaea (Figs. 28G, 28H, and 28I), the anterior connection between the process and the main body of the premaxilla begins to degenerate until only an isolated splint of bone remains. How much of the variation is true difference between genera is not known, but it is evident that a large amount of the observed variation is age.

Astrapia (3), lacking; *Cicinnurus* (6), lacking, a hint of the process in one specimen; *Craspedophora* (1), process partly fused; *Diphyllodes* (8), lacking; *Epimachus* (2), partly fused; *Lophorina* (6), partly fused to completely fused; *Loria* (1), lacking; *Manucodia* (5), present in two specimens, lacking in the others; *Paradisaea* (25), present in 23 specimens, degree of fusion varies, lacking in the other two; *Parotia* (5), partly fused to completely fused; *Phonygammus* (2) slightly fused; *Ptiloris* (1) partly fused; *Scleucides* (5), lacking; *Semioptera* (1), lacking. Checked with Mayr (MS for Peters' Check-list).

Corvidae

The process is lacking (= fused) in the adult crow; the observed variation in the degree of fusion is most likely due to age.

Calocitta (1); *Corvus* (34); *Crypsirina* (2); *Cyanocitta* (13), faint indication of a process in one specimen; *Cyanocorax* (10); *Garrulus* (2); *Kitta* (10); *Nucifraga* (3); *Perisoreus* (6); *Pica* (3); *Ptilostomus* (4); *Pyrrhocorax* (1). Process lacking. Checked with Amadon (1944).

EVOLUTION OF THE PALATINE PROCESS OF THE PREMAXILLA

The discussion of the evolution of the palatine process will, by necessity, be divided into two parts: (a) the general evolutionary principles involved; and (b) the evolutionary pathways traversed by the process (Fig. 29). I am interested here in determining how the palatine process has evolved—how it has changed from one condition to another—not in its actual phylogeny. It is, nevertheless, necessary to consider certain questions that are closely associated with problems of phylogeny, namely whether independent origin plus parallel evolution and reversal of evolution have played important roles in the evolutionary history of the palatine process. Throughout the discussion, the palatine process will be considered as a morphological structure independent of taxonomy, but it will always be integrated with the other structures of the character complex to which it belongs. These evolutionary conclusions are, of course, speculative with the weakest link in the chain of evidence being the functional conclusions. If future empirical studies on the function of the jaw mechanism in birds prove the functional deductions to be wrong, then these evolutionary conclusions also may well be wrong.

Evolutionary principles. A discussion of some basic evolutionary principles may seem to be out of place in this paper and even to be totally unnecessary. Yet in recent papers on avian anatomy and classification, there is a distressing lack of understanding and appreciation of evolutionary principles underlying morphological change. Mayr (1955, 1958) alludes to this problem and discusses some of the basic principles. The reader should consult these papers and the general treatises on major evolutionary change, such as Sewertzoff (1931), Simpson (1953), and Remane (1956), for a more complete coverage of this topic. Yet no single book or paper includes a discussion of all of the principles pertinent to the evolution of the palatine process. These principles will, therefore, be discussed to avoid any possible confusion in their meaning and use in the present paper. I shall restrict my remarks to the evolution of single characters and shall omit those principles, such as "mosaic evolution" and "key innovations," which apply to the evolution of species or groups.

a) Genetic potential: The members of a taxonomic group are basically similar in their genetic compositions which tend to change in a similar fashion. The similarity of the genetic composition and change depends upon the degree of relationship; the closer the relationship, the closer is the degree of genetic potential. This bipartite principle is one of the most important underlying the evolution of both single structures and taxonomic groups — in fact, it is basic to many other evolutionary concepts, including those to be discussed below — yet it is one of the least understood and appreciated concepts of evolution. Although brief, one of the best discussions of this concept can be found in Mayr and Vaurie (1948, p. 246) who conclude that: "Parallelism in evolution must be accounted for by such basic similarity of the germ plasm." Simpson (1953, pp. 348-349) alludes to this principle when he considers the problem of how related groups can acquire the same adaptation independently (i.e., the development of the mammalian jaw articulation in five different lines of therapsid reptiles). Again, Amadon (1956, pp. 15-16) suggests that some of the parallelism in the starlings has been facilitated by the genetic potential of this family.

The evidence supporting the concept of genetic potential is relatively simple and well known to most biologists. First, if there is a direct correlation between the genotype and the phenotype, then a group of related and structurally similar forms would have to be similar genetically. This statement should be

reversed to read that a group of related and genetically similar forms would be similar in their phenotypical expression. However, since the genetics of most groups has not yet been worked out, we must use the more awkward converse. Second, it is well known that, although the occurrence of gene mutations is random, their direction is not random. A gene can mutate only to one of the several alleles found at that chromosomal site; the limitation is most probably imposed by the physical and chemical structure of the gene. Third, the mutant gene must act in harmony with the rest of the genotype if it is to have a selective advantage. Therefore, one can conclude that all of the Passeres are similar genetically and that a structure could change only in a rather limited number of ways. The palatine process of the premaxilla would, then, have a similar genetic basis in all of the Passeres and could change, both genetically and phenotypically, in a limited number of ways.

b) Developmental potential: Many structures are present at some time during development and disappear as visible structures in the adult, a phenomenon especially characteristic of the avian skeleton. Although these structures are "absent" in the adult, they must be regarded as being present in the species because their genetic basis is present and they appear in every generation in the developing animal. Why these structures are present only in the embryo—whether they have a role in development, or are the remnants of degenerating structures—is a most important question, but it is not pertinent to this study. The important thing is that the potential for the structure is present and that the structure could be restored or retained in the adult whenever selection would demand it. The evolution of a structure involving developmental potential may exhibit certain features which are more apparent than real. First, the sudden appearance of the structure may appear to be the result of a single large mutation and second, this mutation may appear to have occurred independently in several groups. Neither of these are correct. The structure, along with its genetical basis, is already present in the embryo and can be retained in the adult by inhibiting or suppressing the factors that cause its normal breakdown and/or disappearance. In the case of an osteological feature, the fusion of a bony process to another bone or its breakdown can be prevented if this process becomes the point of attachment of a muscle or a ligament. This is exactly what has happened in the evolution of the free palatine process. The process is present in all Passeres although it is absent as a

visible structure in the adult, but can "appear" in any family as a free palatine process if part of the *M. pterygoideus* takes origin from it.

c) Preadaptation: A preadapted structure is one whose form will allow it to assume a new function whenever need for that function should arise (Bock, 1959). The new function does not have to be related in any way to the original function of the preadapted structure. Its position along the palatine and the fact that it fuses to that bone relatively late in ontogeny pre-adapts the palatine process for the function as the origin for part of the *M. pterygoideus* as seen in the cardinals and several other families of passerine birds.

d) Multiple pathways of evolution: The same selection force acting on several groups of animals may elicit different adaptive responses depending upon the genotypic and phenotypic differences between these groups. These different adaptive responses would be the multiple pathways of adaptation or evolution. The basis for multiple pathways lies in the fact that there are usually several ways to achieve the same functional goal (see Simpson, 1953, pp. 179-181; and Bock, 1959). For example, at least two different methods for cracking seeds have evolved in the *Passeres* and each has its own special anatomical modifications including the structure of the palatine process of the premaxilla. Within this primary dichotomy of multiple pathways for seed-cracking, are secondary and probably even tertiary or lower levels of multiple pathways. If, for instance, a passerine bird has "chosen" the nutcracker method of seed-cracking, then there are a number of different ways of evolving the necessary adaptations, e.g., differential development of the several adductor and protractor muscles. The most important consequence of multiple pathways for the functional anatomist and the evolutionist is that morphological differences between the adaptations for the same function are non-functional and hence non-adaptive in terms of that particular function. Only differences between the structure in the ancestral and descendent species are functional and thus adaptive. Therefore, one cannot assume that all of the morphological differences between contemporary groups are adaptive differences. It must be emphasized, however, at this point, that multiple pathways can be discussed in terms of only one function, or in terms of only one selection force. The differences between the adaptive responses for one selection force may be adaptive in terms of other functions. Thus one condition may evolve to

another under the influence of these other selection forces. For example, although the differences between the adaptive responses — the nutcracker method and the vise method — for seed cracking in the Passeres are non-functional in terms of seed cracking, they are probably functional and adaptive in terms of insect catching. Thus the “vise structure” could change to the “nutcracker structure” and vice versa under the influence of selection forces associated with insect eating, but could not change under the influence of the selection force associated with seed cracking.

e) Independent origin and parallel evolution: These two evolutionary principles are independent in that one does not depend upon the other; however, because both are dependent upon the principle of genetic potential and because they frequently occur together, they are best discussed together. The term “independent origin” refers to the separate evolutionary origin of the same structure in different taxonomic groups, as for example the free palatine process in the flycatchers and the cardinals. This may be the result of *de novo* appearance of the structure because of similar genetical changes or it may be the retention of an embryological structure in the adult. Separation of these possibilities is impossible without detailed genetical and embryological investigations. “Parallel evolution” is similar evolution of a structure in different taxonomic groups, i.e., the structure undergoes the same series of changes. Clearly then, if the families of passerine birds have a basically similar genetical potential for a certain structure, that structure could arise independently and evolve in a parallel fashion if the same selection forces acted on the members of several families. Yet structures that have arisen independently do not have to undergo a subsequent period of parallel evolution and vice versa. Many examples of independent origin and of parallel evolution of the palatine process can be cited. Some notable ones could be the free palatine process in the cardinals. *Furnarius* and some of the tyrant-flycatchers, and the lateral flange in the carduelines, the ploceids, *Oryzoborus* and *Psittirostra*.

f) Convergence: Convergence occurs when formally dissimilar structures or structures in unrelated taxonomic groups become similar to one another. There is no sharp break between parallelism and convergence, and indeed some workers do not distinguish between the two concepts (see, however, Haas and Simpson, 1946, for a discussion of this problem). However, as there are several important differences between typical convergence and typical parallelism, I shall distinguish between them.

Cases of convergence in the palatine process are somewhat difficult to separate from parallelism because we know so little about the relationships of the passerine families. One example may be the evolution of the lateral flange in the carduelines and the ploceids if these groups are unrelated.

g) Reversal: Reversal is evolutionary change of a structure to a condition that is similar to the primitive or original structure. The sequence would be primitive — specialized — secondarily primitive. The question of whether reverse evolution means an exact backwards change involving the same steps and genetic changes is a moot if not a ridiculous problem. Most likely, reversal does not involve the same genetical changes, but this is of little importance. The important consequence of reversal is that a secondarily primitive structure frequently cannot be distinguished morphologically from an originally primitive structure! These morphologically similar, but evolutionary-wise different conditions usually can be separated from one another only after the phylogeny of the taxonomic groups has been determined. Reversal in the evolution of the palatine process had probably occurred many times, as for example, when an insectivorous group has evolved from a heavy-billed group. An example may be the evolution of the Drepaniidae from the Carduelinae with the loss of the lateral flange in the thin-billed members of the Hawaiian honey-creepers.

The most important feature of these several evolutionary phenomena, especially independent origin, convergence and reversal, is the frequency of their occurrence. If they were of rare occurrence during the evolution of a taxonomic group, then they would be of only minor importance. As their frequency increases, so does their importance in evolutionary and taxonomic studies as well as the difficulty in untangling the phylogeny of a group, but this increase in importance and difficulty is a rapid geometric increase. It is my belief that these phenomena were of common occurrence during the evolution of birds because birds share a very similar genetic potential. This appears to be especially true in the Passeres in view of their great similarity in structure. It is difficult, however, to cite indisputable examples of these phenomena in the case of the palatine process. The problem stems from the fact that we know so little about the phylogeny of the Passeres that we can never be certain, in many cases, whether similarity in the palatine processes of two families is the result of common ancestry, parallelism or convergence. Nor can we determine at this time the frequency of independent

origin and reversal. It is always better to be cautious in taxonomic studies, hence I shall stress the need to consider these phenomena at all times.

Evolutionary history of the palatine process.

a) Primitive form: The primitive condition of the palatine process of the premaxilla is that of the process lying along the lateral edge of the palatine and more or less fused with that bone — the normal condition of the palatine process as seen in the crow or the white-throated sparrow. It is impossible to determine whether the palatine process of the premaxilla was completely or only partly fused with the prepalatine process of the palatine in the ancestral passerine bird, but this is of little importance. Change from an incompletely fused process to a completely fused one or vice versa is exceedingly simple and has probably occurred repeatedly during the evolution of the Passeres. Two bits of evidence support the conclusion that the normal palatine process is the primitive condition. First, this is the condition found in most passerine birds as well as in most other birds. If the normal palatine process was not the original condition in the Passeres, one would have some difficulty explaining its present-day distribution in the passerine families. Second, all other conditions of the palatine process in the passerines appear to be specializations for some particular mode of feeding. This is certainly true for the free palatine process and the lateral flange on the prepalatine process.

b) Selection forces: The factor most frequently omitted from discussions of the evolution of a structure is the set of selection forces acting on that structure. In the case of the palatine process, the primary function and hence the primary selection force is insurance of a firm connection between the palate and the upper jaw. This selection force may not have been responsible for the origin of the palatine process which probably took place some time in the early history of the birds, if not earlier. However, this selection force is responsible for the maintenance of the palatine process in birds and for some of the variation in the degree of fusion with the prepalatine process. All modifications of the palatine process in the Passeres must always fulfill the demands of this primary selection force. The secondary functions and hence the secondary selection forces acting on the palatine process are independent of each other, and indeed they apparently cannot act together in harmony. One of the secondary selection forces is associated with the vise method of cracking seeds and selects for the fusion of the palatine process

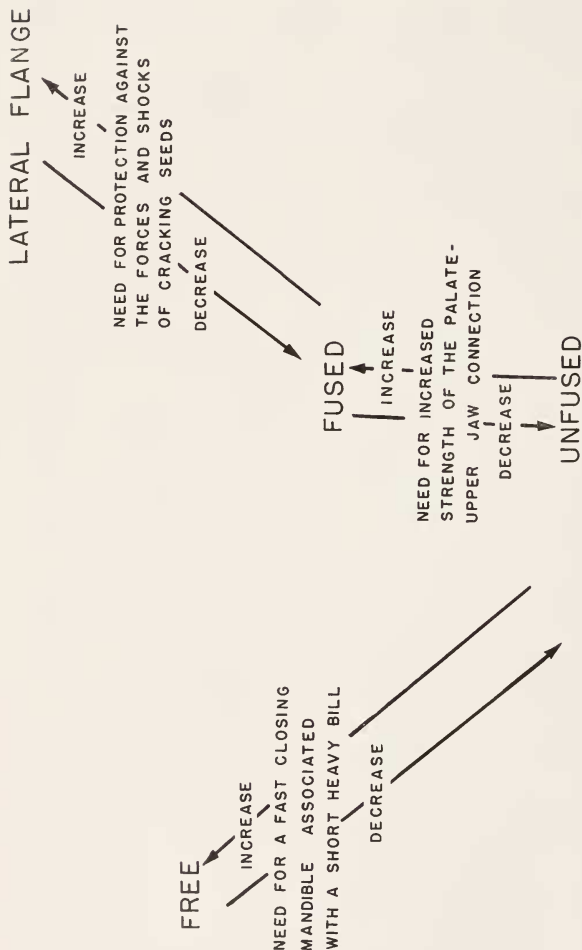


Figure 29. Dendrogram showing the evolutionary pathways in the evolution of the palatine process. The selection forces bisect the lines leading from one condition to another. See the text for further explanation.

with the prepalatine process and the development of a lateral flange at the site of fusion. The other secondary selection force is associated with a fast closing mandible during the early phases of closing the bill and selects for a free palatine process from which a portion of the *M. pterygoideus* originates.

c) Maintenance of the palatine process: During most of the evolution of the Passeres, there was little or no change in the structure of the palatine process. Slight changes in the strength of the primary selection force had no doubt occurred which could account for some of the variation in the degree of fusion between the palatine process and the palatine, as for example, in the *Dendrocolaptidae* and the *Pipridae*. Parallelism in the amount of fusion of the palatine process or in its degeneration as an isolated splint of bone lying along the palatine are probably common, as are reversals in the trends of fusion or breakdown. It is impossible to determine whether the normal condition of the palatine process in any group of passerine birds is originally primitive or secondarily primitive or even, as will be shown later, if the group had passed through an earlier stage having a more specialized type of palatine process.

d) Evolution of the free palatine process: The evolution of the free condition of the palatine process is dependent upon changes in the *M. pterygoideus ventralis lateralis*. This muscle becomes larger in some passerine birds with the lateral superficial fibers extending forward along the palatine. It has been shown that the forward extension of these fibers has several important functional consequences in addition to the increased strength of the muscle. These fibers would be longer than all other fibers of this muscle; hence it would appear reasonable to suggest that their action is faster and over a longer distance than the shorter fibers of the *M. p. ventralis lateralis*. It has been pointed out above that the insertion of these superficial fibers is such that their main function is to raise the mandible during the early phases of closing the bill. This is a rapid, but not a very powerful closing of the bill. Once the origin of the superficial fibers reaches the anterior end of the palate, the palatine process can assume the role of the point of origin. The detailed steps leading up to this are outlined below.

The tendon of this superficial bundle runs forward along the palatine to attach somewhere along that bone or at the junction between the palatine and the premaxilla in the more advanced forms. This tendon is closely associated with the periosteum of the palatine, especially where the tendon takes

origin from the palatine. In the more advanced forms, the tendon takes origin from the periosteum of the palatine process. As the superficial bundle of the *M. pterygoideus* increases in size, its tendon shifts away from its original position along the palatine until it is free of the palatine for most of its length. Finally, the tendon meets the palatine bone at a slight angle. At this time, the tendon usually originates from the fused or the partly fused palatine process, although it has not yet influenced the position or the fusion of the palatine process which is still only under the control of the primary selection force. But, as has been pointed out above, the palatine process fuses to the palatine bone relatively late in ontogeny. Thus, if the tendon of the superficial bundle originates on it and if this tendon approaches the palate at a slight angle, then the distal end of the palatine process would be "pulled" away from its original position along the palatine to a new position in the space between the palate and the jugal bar. The distal end of the palatine process, then, could not fuse to the prepalatine process. However, the anterior part of the process still fuses with the palatine, which apparently fulfills the demands of the primary selection force. In its new position, the palatine process would be free of the palatine and at a slight angle as well as a little ventral to it. The process would, thus, lie exactly in line with the longitudinal axis of the superficial bundle of the *M. pterygoideus* and hence would be in the most effective position as the point of origin for that muscle. Once the palatine process is free of the palate, some ossification of the tendon may occur, thereby lengthening the process. Proof of this point is exceedingly difficult to obtain because ossified tendons are practically indistinguishable from normal bone, both macroscopically and microscopically. However, this is a minor point with no direct bearing on the evolution of the free palatine process.

The development of the superficial bundle of the *M. p. ventralis lateralis* is an exceedingly simple evolutionary change and has probably occurred independently many times during the evolution of the Passeres. Here is the basis for the independent origin, parallel evolution and even convergence of a free palatine process. The normal palatine process, no matter whether it is incompletely or completely fused to the prepalatine process, is preadapted to evolve into the free process with the appearance of the selection forces favoring this condition (i.e., the development of the superficial bundle of the *M. pterygoideus*). The appearance of a free process in a group that does not have a

visible palatine process in the adult is facilitated by the genetic and developmental potential alluded to above.

Loss of the free palatine process and reverse evolution back to the normal condition will occur whenever the *M. pterygoideus* changes back to its original condition, i.e., by losing the superficial bundle of fibers. The loss of this separate bundle is not associated with decrease in the strength of the bite, but would occur if the bird no longer needed a fast closing bill or had developed a more efficient way to close the bill rapidly, as, for example, by lengthening the bill and palate which automatically lengthens the *M. pterygoideus*. In fact, the only birds with a free palatine process or with tendencies toward this condition are those which must combine a short bill with rapid closing. If a group had lost the free palatine process and returned to the normal condition, there would be no way of distinguishing the secondary normal condition from the primary or primitive normal condition. Thus we cannot determine which of the tanagers possessing a normal palatine process has evolved from ancestors possessing a free palatine process. Nor can we determine whether or not the ancestors of the emberizine finches had a free palatine process. Such determinations must wait until the true phylogeny of these groups has been established.

e) Evolution of the lateral flange: The evolution of the lateral flange is far simpler than the evolution of the free palatine process. Most, if not all, birds have a membrane stretching between the prepalatine process and the jugal bar or the lateral edge of the upper jaw. This membrane is part of the lining of the roof of the mouth. Ossification of this membrane is the easiest and probably the most efficient way of achieving additional protection in this region of the skull against the shocks that may accompany cracking seeds by means of the vise method. Such ossification would result in an automatic fusion of the palatine process with the palatine if it was not already fused, and in the subsequent development of the lateral flange as seen in the cardueline and the ploceid finches. Additional protection such as the development of overlying pads of rhamphotheca can evolve after the development of the lateral flanges. I need scarcely point out the ease with which the lateral flange could arise independently in different groups and evolve in a parallel fashion or converge depending upon how distantly related the groups were. Also, reversal can occur when the selection force for protection against the forces and shocks of feeding is no longer in existence. The secondary normal palatine process, such

as may occur in some of the thin-billed Drepaniidae, is indistinguishable from the primitive normal palatine process.

TAXONOMIC VALUE OF THE PALATINE PROCESS OF THE PREMAXILLA

With the aid of the information on the evolution of the palatine process gathered in the preceding section, we can proceed to the evaluation of its taxonomic significance—this being the ultimate aim of any study of a taxonomic character. The taxonomic value of the palatine process in relating families of passerine birds will be evaluated first, followed by a discussion of the relationships of certain families and genera based on the evidence of the palatine process and, in part, the jaw muscles. I wish to emphasize that these discussions on the relationships of the various families and genera are only suggestions based on the available data; they are not hard and fast opinions or conclusions on the affinities of these groups. Here again, I might reiterate my earlier statement that it is my belief that we do not have and probably will not have for many years, the necessary body of evidence on which to base conclusions on the relationships within the Passeres.

Taxonomic value. The taxonomic value of a structure depends, as has been mentioned above, upon the nature of the controlling selection forces. If these selection forces have a tight control over the structure and if they have arisen repeatedly and changed direction often during the evolution of the group, then that structure would have very little taxonomic value in that group. One could argue about the degree of control on the palatine process by the several selection forces guiding its evolution, but it is reasonable to assume that these selection forces exert a fairly tight control on the palatine process. There is little question, however, about the fact that the several controlling selection forces have arisen repeatedly and have reversed their direction numerous times during the evolution of the perching birds. Therefore, I would conclude that the palatine process of the premaxilla has *little or no* value in showing relationships between families of passerine birds or in placing problem genera into the correct family. Here, I must disagree with Tordoff, who concluded (1954a, p. 33) that the palatine process provides a good clue to relationships in the New World nine-primaried oscines. The taxonomic changes advocated by Tordoff are consequently not justified on his evidence and should not be accepted unless supported by other evidence. A detailed discussion of these changes will be given below.

The Passeres and the New World nine-primaried oscines. The palatine process of the premaxilla does not offer any clues which might help solve the problem of the relationship of the Passeres to other orders, or the problem of the major groupings within the Passeres. I should mention again that the results of this study neither support nor refute any of the arrangements proposed in recent years of the Passeres or of the Oscines. There are, however, parts of each system that are not in agreement with the available evidence provided by the palatine process and the jaw muscles. For example, the separation of the Fringillidae (Carduelinae + *Fringilla*) from the Emberizinae in both Mayr and Greenway's, and Amadon's lists does not agree with the similarity in the configuration of the jaw muscles of these groups. The separation of some of the New World nine-primaried families in Wetmore's arrangement does not appear to be justified in view of the great similarity of these families. In fact, all of the available morphological evidence indicates that the nine-primaried oscines are a monophyletic group. The structure of the palatine process of the premaxilla, although it does not provide any strong proof for a monophyletic origin of the nine-primaried group, at least does not argue against it. However, the relationships within this assemblage are exceedingly complex and for all practical purposes, are completely unknown. The probable ancestral group and the directions of evolution within the group are anyone's guess. In fact, the family limits cannot be defined with any degree of certainty; hence many problem genera cannot be allocated to the proper family or subfamily. Although much work has been done toward the clarification of the relationships between the nine-primaried families, much more must be done before the problem is solved; however, it is hoped that in the future, more attention will be paid to the group as a whole and not to whether this family is allied to that family, or where a certain problem genus should be placed.

Vireonidae. The vireos are, in the opinion of many workers including myself, the most likely representatives of the ancestral nine-primaried stock. The reasons for this choice are negative rather than positive, namely that the vireos are relatively generalized insect-eaters while most of the other nine-primaried families are apparently specialized in one way or another. Rejection of Tordoff's hypothesis that the free palatine process as found in the cardinals is the primitive condition eliminates one of the serious objections to the vireos being the ancestral nine-primaried oscines. The vireos have a normal palatine process, a relatively

unspecialized set of jaw muscles, and a tenth primary (only some species), all of which support the hypothesis that the vireos represent the ancestral nine-primaried stock. Yet, this evidence is not very conclusive and much more is needed to verify this hypothesis.

Vireolanius and *Cyclarhis* have been included in the Vireonidae. They appear to be heavy-billed vireos with a more heavily fused palatine process. It should be pointed out, however, that we do not have a single, thorough, study evaluating the morphological differences between these genera and the vireos.

Parulidae. The arguments for the origin of the wood-warblers either from the vireos (Beecher, 1953, p. 307) or from the emberizine finches (Tordoff, 1954a, 1954b, p. 278) are based on rather weak evidence. Tordoff's argument stems from his insistence that the free palatine process is the primitive condition and that evolution proceeded mainly or only in the direction of reduction and loss of the palatine process. If the wood-warblers arose from the vireos, which is not an unlikely hypothesis, then Beecher may be correct in stating that the pinnate muscles of the warblers (as for example, the *M. pseudotemporalis superficialis* which serves to raise the mandible during the early phases of closing the bill) may have given them an advantage over the vireos which have only parallel-fibered muscles. Pinnate muscles do not develop only in response to selection for increased strength; they may have other functions, perhaps speed, which we do not suspect and thus could develop in response to selection for these functions. However, it must be emphasized that there is very little evidence available that may shed light on the origin and affinities of the Parulidae.

Icteridae. Again the arguments advanced by Beecher (1951a, 1953) and Tordoff (1954a) for the origin of the Icteridae from the Emberizinae are inconclusive; the necessary evidence is simply not available. Beecher's statement that the cowbirds, *Molothrus*, represent the ancestral stock of the icterids is pure speculation. The diekeissel, *Spiza*, will be discussed below with the cardinals.

Coerebinae. The New World honey-creepers (Coerebinae) provide an excellent example of the hodgepodge nature so characteristic of the nine-primaried families. Beecher (1951b) is probably completely correct in pointing out the polyphyletic nature of the honey-creepers, but I am not convinced that he has solved the convergence problem and clarified the affinities of the coerebid genera. It is likely that most of the honey-creepers have evolved

from the wood-warblers or from the tanagers, but whether there are two clear-cut groups, the Coerebini (nectar-feeding warblers) and the Daenini (nectar-feeding tanagers), is another question. Beecher's interpretations of the similarities in the jaw muscles between the Coerebini and the warblers and between the Daenini and the tanagers are not convincing (see above, p. 400, for a general discussion of Beecher's work). Of the other evidence — the horny palate relief, plumage pattern and differences in the manner of feeding — presented by Beecher, only the nature of the ridges on the horny palate appear to have any value in showing affinities. However since I have not studied this feature, I do not feel qualified to evaluate it. It is interesting that Tordoff (1954a, pp. 30-31) has found the palatine process to be absent in the Coerebini, as in the warblers, but present and more or less fused with the palatine in the Daenini, as in the tanagers, thereby supporting Beecher's earlier conclusion. I have found much variation in the degree of fusion between the palatine process and the palatine bone in the honey-creepers, but was not able to ascertain any differences in the degree of fusion between the genera assigned to the Coerebini and those assigned to the Daenini by Beecher. In view of this inconclusive evidence, I would agree with Mayr and Greenway (1956) who recognize the old group "Coerebinae" even though they realize that it is of polyphyletic origin. The only alternative solution at the present time is to list the genera of honey-creepers as *genera incertae sedis*. However, since both alternatives accomplish the same end result, it is best to retain the old "Coerebinae" until we have discovered the true affinities of its genera.

Cardinalinae and Tanagrinae. The cardinals and the tanagers are so similar to one another in many respects and seemingly grade so imperceptibly into one another that they are best discussed together. Beecher (1953) and Tordoff (1954a) agree that the cardinals are related to the tanagers, but disagree on the direction of evolution. Nelson (1954) agrees that the two groups are related on the basis of similarity in the pneumatic fossa of the humerus, but believes that these families are not related to the Emberizinae (see Berger, 1957, pp. 266-267, for a discussion of the pneumatic fossa of the humerus). There cannot be any question that the cardinals and the tanagers are very similar morphologically, but I doubt that the evidence advanced by these authors proves that they are closely related within the nine-primaried assemblage. Nor can the evidence be used to distinguish between the cardinals and the tanagers, or between

either or both families and the emberizine finches. Mayr (1955, p. 34) pointed out that the direction of evolution in the nine-primaried oscines, and especially in these three families, is in doubt. This is still true. It seems certain that the free palatine process of the cardinals is not the primitive condition in the New World nine-primaried oscines, but we cannot tell whether the emberizine finches gave rise to the tanagers or vice versa, or whether the cardinals gave rise to the tanagers or vice versa, or whether these groups are more distantly related. We cannot even be sure that the cardinals and the tanagers are good taxonomic groups. For these reasons, I do not see the point of worrying about the correct position of the numerous problem genera — especially those from tropical regions — of the nine-primaried finches. What difference does it make whether *Saltator* is a tanager or a cardinal, or whether *Chlorospingus* and *Oreothraupis* are tanagers or emberizine finches when we have no idea of the limits of the familial groups.

One genus, *Spiza*, must be discussed because of the importance placed on it by Tordoff. In both of his papers (1954a, 1954b, p. 218), Tordoff placed *Spiza* in the Cardinalinae and claimed that it represents the ancestral fringillid and consequently the ancestral nine-primaried stem stock better than any other living genus. This opinion is based on his belief that the free palatine process is primitive; his other reasons supporting this opinion are incidental. On the other hand, Beecher (1951a, 1953, p. 309) claimed that *Spiza* is an icterid on the basis of the configuration of the jaw muscles, although he did not figure these muscles in either paper. There is no question about the structure of the palatine process in the dickeissel; it is free as in the cardinals, but this is far from proof that it is a member of the Cardinalinae. Unfortunately, I have not been able to dissect the jaw muscles of the dickeissel, but I would be most surprised if a superficial bundle of the *M. pterygoideus ventralis lateralis* did not originate from the free palatine process. It is of interest that in some icterids, such as the grackle, the *M. p. ventralis lateralis* sends a lateral tendon forward for a short distance along the palatine. This indicates that the potential for developing a separate superficial bundle of the *M. pterygoideus* and a free palatine process may be present in the icterids. Most of the other evidence cited by both Tordoff and Beecher is likewise inconclusive. For example, the similarity in color pattern between the dickeissel and the meadowlark may well be convergence because of their living in the same habitat, as has been pointed out by Friedmann

(1946). New and different evidence is needed before the affinities of *Spiza* are clarified.

The swallow-tanager, *Tersina*, scarcely deserves a separate discussion. In the structure of the palatine process, this genus appears to be a tanager, but whether it should be placed in that group or in a group of its own is another problem. It is interesting that the true swallows usually have an unfused and quite distinct palatine process. Although I have not dissected the jaw muscles of these groups (the one swallow I examined was a damaged specimen), I would suspect that a part of the M. pterygoideus took origin from the palatine process and had the function of raising the mandible rapidly, as in the cardinals and the tanagers. I also suspect that such an arrangement of the M. pterygoideus will be found in some of the tyrant-flycatchers.

Fringillidae and Emberizinae. The Fringillidae of older authors are, with little doubt, one of the most controversial families in the nine-primaried complex. Most of the recent arguments about relationships in the nine-primaried oscines center about the Fringillidae or start with them. This family according to the older classifications, e.g., Wetmore, is composed of the Emberizinae, the Cardinalinae and the Fringillinae (including the cardueline finches). Many recent workers suspected, however, that this family is polyphyletic in origin and have set out to uncover the true affinities of the several subfamilies. The conclusions of the various authors differ radically, but they need not be summed up here. The only one that will be considered is Tordoff's conclusion that the cardueline finches (excluding *Fringilla*) do not belong to the nine-primaried group, but are related to the ploceids. *Fringilla*, according to Tordoff, is a primitive emberizine finch. The only recent modification of Tordoff's conclusions has been that of Mayr, *et al.* (1956) who concluded that *Fringilla* is closely related to the carduelines. Because I believe that Tordoff's reasons for separating the cardueline finches from the nine-primaried assemblage are baseless, it is necessary to re-examine the entire problem of the "Fringillidae." In doing so, I will use only the morphological evidence, especially that supplied by the cranial anatomy.

There seems to be little disagreement about the conclusion that the cardinals are closely related to the emberizine finches. If the cardinals are included in the "Fringillidae," then the tanagers will most likely also have to be included. However, in view of the inconclusive evidence pertaining to the affinities between the cardinals and the emberizine finches, this aspect of the

problem will be dropped and attention will be concentrated on the relationships between the emberizine finches and the carduelines plus *Fringilla*.

Mayr, *et al.* (1956) have presented much evidence pointing to a close affinity between *Fringilla* and the cardueline finches; one of the most serious disagreements was the unfused palatine process in *Fringilla* as compared to the fused process and the lateral flange in the carduelines. The results of the present study have shown that the presence of an unfused palatine process in *Fringilla* and its apparent absence in the carduelines does not necessarily mean that the two groups are unrelated, as supposed by Tordoff. Although *Fringilla* does not possess a lateral flange, its jaw muscles are almost identical to those in the cardueline finches as has been reported earlier by Fiedler (1951) and Beecher (1953). The most distinctive feature of the cardueline jaw musculature is the enlarged medial portion of the M. pseudotemporalis superficialis. *Fringilla* agrees completely with the carduelines in this feature. The major difference between the jaw muscles of the two groups is the poorly developed M. adductor mandibulae in *Fringilla* which is similar to that found in the emberizine finches (see Fiedler, 1951, p. 242). This muscle is highly developed in the carduelines with two parts expanding over the side of the skull. In addition, some of the emberizine finches, e.g., the fox sparrow, tend toward the cardueline finches in the structure of the M. pseudotemporalis superficialis and the M. pterygoideus. Thus in several aspects of the bony palate and the jaw musculature, *Fringilla* is intermediate between the emberizine and the cardueline finches, but it is closer to the carduelines. On the other hand, none of the ploceid or estrildid finches, to my knowledge, tend toward the cardueline arrangement of the jaw muscles, especially in the very distinctive condition of the M. pseudotemporalis superficialis. I must emphasize, however, that I have dissected only the house sparrow (*Passer*) and the heavy-billed *Colinus passer* and examined Beecher's plates of the jaw muscles in the ploceid and estrildid finches so that my sample of these finches is quite small.

Although no definite conclusions on the relationships between the fringillid, emberizid and ploceid finches can be based on the available evidence from the cranial morphology, several hypotheses may be advanced. I cannot see any indications of a relationship between the carduelines plus *Fringilla* and the ploceids or the estrildids, as advanced by Tordoff. Because of the intermediate position of *Fringilla* in many features of the cranial

anatomy, it does seem reasonable to suggest that the emberizine finches gave rise to the carduelines through a *Fringilla*-like group. The cardueline radiation could have eliminated an earlier *Fringilla* radiation except for *Fringilla* itself. If this hypothesis is correct, then the Fringillidae of Wetmore is a monophyletic group and the similarity between the Carduelinae and the Estrildidae and the Ploceidae in the structure of the lateral flange would be convergence. It is entirely possible, however, that the carduelines plus *Fringilla* are related to the ploceids or the estrildids and that the similarity between the fringilline finches and the emberizines in the structure of the jaw muscles is due to convergence.

Drepaniidae. The origin of the Hawaiian honey-creepers remains a deep mystery even after many workers have devoted much time to this problem. One of the main reasons why the origin of the Drepaniidae has eluded ornithologists is because the structures so far studied were those which could never supply conclusive clues to their affinities. Although Drepaniidae constitute one of the best examples of adaptive radiation in feeding methods in the Passeres, the investigations of most workers on the origin of this group are based on characters associated with feeding methods. The present study of the palatine process has shed some light on this problem and I wish to offer the following ideas as a suggestion.

The group that gave rise to the Hawaiian honey-creepers had to have three characteristics. They had to be birds that wander in flocks, preferably erratically, over long distances, and breed at the place to which they have wandered. Of all the possible ancestral groups, the cardueline finches are the only ones that possess all three attributes. Here again, it must be pointed out that the objection to the carduelines as the ancestral drepaniids, presented by Tordoff, has been removed. It is quite possible that a cardueline finch or a member of its ancestral group had reached the Hawaiian Islands and gave rise to the Drepaniidae, a hypothesis already advanced by Sushkin (1929). The possession of a finch bill, even a heavy cardueline bill with its lateral flanges on the prepalatine process, does not present any problem for this hypothesis. The lateral flanges can be lost whenever the selection forces for them are eliminated or reversed. It is interesting that the bones of the palate and upper jaw of the heavy-billed genus *Psittirostra* are identical to those found in the large-billed carduelines. According to Beecher (1953, p. 311), the jaw muscles, including the expanded medial part of the *M. pseudotemporalis*

superficialis, of *Psittirostra* are almost identical to those of the cardueline finches. This suggested origin of the Drepaniidae is speculation and must be verified or rejected on additional evidence. I have offered it mainly to counteract the trend of thinking that the Hawaiian honey-creepers had to originate from a thin-billed member of the nine-primaried oscines.

CONCLUSIONS

A sharp distinction was made in the beginning of this paper between comparative studies of many characters in two or a few passerine families and comparative studies of a single character or character complex in the entire order Passeres, with the tacit, but clear implication that the former rarely led to conclusive taxonomic results. It is now necessary to evaluate the conclusions which may be gained in the latter type of study.

The first thing that probably comes to the mind of most readers is the highly speculative and inconclusive taxonomic results presented above. In fact, the only definitive conclusions were negative ones. These inconclusive results are scarcely surprising in view of the fact that they are based on the evidence supplied by a single character complex. Nevertheless, these are not very encouraging results for a taxonomic paper. Let us look, however, on the positive side of the ledger. This study has provided detailed knowledge of the structure and variation of the palatine process along with some information on its embryological origin and a fairly good idea of its functional significance. With this information, it was possible to gain a reasonably accurate picture of the evolution, although not of the actual phylogeny, of the palatine process. Such data, especially those on the evolution, are only rarely supplied by comparative studies of two families. Yet one can ask, what can be done with this information? If only a few inconclusive taxonomic results can be reached after such an extensive study as the present one, then why continue with these studies if one is primarily concerned with the classification of the perching birds? With comparative studies of families, we at least know how different these families are. Would it not be best to return to these studies?

The answer, or at least my answer, to the last question would be no. Still there is no reason to continue these extensive studies of single characters for the sake of the taxonomic deductions that may be reached in individual works. But then, why do taxonomic conclusions have to be offered at the end of every

taxonomic study? Is it not enough to present the data in such a way that they can be used to help formulate sound judgments of affinities when enough data have been gathered? With only a single study, such as the present one, very little if anything can be learned about the evolution and relationships of the Passeres. Perhaps a bit more can be learned with two or three studies. However, with several dozen such works, there would be a good chance of unraveling the entire evolutionary history of the recent Passeres. The evolution of the individual characters could be pieced together to form an overall evolution of the Passeres. Use of a large number of different characters will reduce the chance of error to an insignificant amount. This overall picture of the evolution of the Passeres will then serve as the basis for a classification of the order. It is my firm belief that a sound classification of the passerine birds can best be reached through a series of single character studies. This is a long and tedious task with relatively few rewards until the central problem is finally solved. But there are no short cuts to the goal, so that the sooner thorough analyses of single characters are begun, the sooner we will have a suitable classification of the Passeres.

SUMMARY

A comprehensive analysis of a single character — the palatine process of the premaxilla — in the Passeres is presented as a basis on which to judge the merits of the "single character study" approach to passerine classification.

The four major conditions — fused, unfused, free, and with a lateral flange — of the palatine process are described.

A history of the past studies is presented in which the origin of the erroneous term "palato-maxillary" for the palatine process is shown.

The embryology of the palatine process in birds possessing the process and in birds supposedly possessing the "palato-maxillary" is compared. It is shown that these terms refer to the same structure in the passerines and hence "palato-maxillary" should be dropped from use since it is the younger term.

The functional significance of the palatine process is discussed with two separate problems in mind. The first is the maintenance of the process in birds. It is shown that the primary function of the palatine process is insurance of a firm palate-upper jaw connection which is associated with the kinetic skull. The second problem concerns the modifications of the palatine

process in the finch-like Passeres. These modifications are associated with certain aspects of seed-eating. Therefore, it is necessary to investigate the correlation between the process and the *M. pterygoideus* (the only muscle attached to the palate), the different ways to increase the force of the bite and the methods by which the several groups of finches crack seeds. It is shown that the free palatine process serves as the point of origin for part of the *M. pterygoideus* and is associated with the nutcracker method of cracking seeds. This is an adaptation for a rapidly closing mandible. The lateral flange is associated with the vise method of cracking seeds, and is an adaptation for protecting the brain and sense organs from the forces and shocks that accompany the cracking of seeds.

Finally, the results of a survey of the palatine process in the Passeres are presented with a résumé of the types of inter- and intrafamilial variation.

The evolution of the palatine process is outlined with a short discussion of the several evolutionary principles that figure in its evolution. The normal condition of the palatine process — lying along the palatine and fused or unfused to it — is assumed to be primitive. Change from the fused to the unfused condition and vice versa has doubtless occurred repeatedly during the evolution of the Passeres. Evolution of the free process from the unfused process is under the control of selection forces for a fast-closing bill, while the evolution of the lateral flange is under the control of selection forces for protection of the braincase. These evolutionary changes can be reversed with a reversal of the selection forces. Apparently, the free process cannot evolve directly into the lateral flange; it must first pass through the normal condition.

It is concluded that the palatine process has little value in showing relationships between families of passerine birds. Some of the problems of relationships within the nine-primaried oscines are discussed, but no definite conclusions are reached.

Although individual studies of single characters, such as the present one, do not lead to definite taxonomic conclusions, it is suggested that comprehensive studies of single characters throughout the Passeres will eventually provide the best basis for understanding relationships within the order and it is urged that more studies of this type be undertaken.

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